

CAMERAEA FROM THE LATE CLASHOONIAN LOVE HOLE MCO,
ALACHUA COUNTY, FLORIDA

by

JON RAN NIKIN

A DISSERTATION PRESENTED TO THE GRADUATE COUNCIL OF
THE UNIVERSITY OF FLORIDA
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE
DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA
1982

ACKNOWLEDGMENTS

Sam and Pat Lane of Archer, Florida have enthusiastically supported the field work of the Florida State Museum on their property for the past six years, beginning with their initial discovery of a Pleistocene bone while utilizing their field. Many people have taken part in the excavation and preparation of the faunal remains from this locality. To all of them I express my deep appreciation. E.H. Telford, of the American Museum of Natural History, allowed me to describe the primate material under his care. This material was also collected through the efforts of many people, notably the late Orin Frick, who guided the collection of the majority of primate material described in this paper. Bill Brown, Jim Linstead and R.V. Smith donated important primate material collected by them from the Bone Valley area to the Florida State Museum. John Willup allowed me to describe a *Fiberless* Research Organization specimen. C. Ray permitted me to study specimens in the Natural Museum of Natural History collections.

D. David Smith directed this study and offered helpful comments, discussion, criticism and support throughout its duration. This study has benefited from conversations with R. Collins, C. Bardefeg, R. Taylor and E. Telford of the American

Journal of Natural History. L.S. Beer, R. Pridmore, B. Reed, S.O. Webb, and B. Wolff critically reviewed this manuscript. Lauren Warwick drew figures 1, 3-8, 11, 25-28, and 32-34. My wife, Christina, drafted figures 10, 12 and 34 and typed this and previous versions of this manuscript. This research was supported by National Science Foundation grants 00370-11540 and 00370-10470.

LIST OF TABLES

Table	Page
1. Measurements taken on <u>Bothriophis</u> level	12
2. Comparison of \bar{L} , length to <u>Bothriophis whitfordi</u> , <u>B. nortoni</u> , and <u>B.</u> level	32
3. Measurements taken on <u>Stenocranius galieni</u>	38
4. Measurements taken on <u>Bothriophis</u> atlas and axis	54
5. Measurements of the sacrum	58
6. Measurements of the humerus	62
7. Measurements of the ulna	65
8. Measurements of the radius	67
9. Measurements of the carpus	68
10. Measurements of metacarpal I	73
11. Measurements (\bar{L} , $\pm \bar{S}$, S.E., \bar{N}) of metacarpals II-IV of <u>Bothriophis</u>	75
12. Measurements (\bar{L} , $\pm \bar{S}$, S.E., \bar{N}) of metacarpals II-IV of <u>Stenocranius</u>	76
13. Measurements of the femur	81
14. Measurements of the tibia	83
15. Measurements of the tarsals	85
16. Measurements (\bar{L} , $\pm \bar{S}$, S.E., \bar{N}) of metatarsals II-V of <u>Bothriophis</u>	89
17. Measurements (\bar{L} , $\pm \bar{S}$, S.E., \bar{N}) of metatarsals II-V of <u>Stenocranius</u>	92
18. Measurements taken on <u>Idioscopus</u> level	107

LIST OF TABLES (CONT.)

<u>Table</u>	<u>Page</u>
19. Measurements taken on <u>Archimedes</u>	164
20. Selected attributes of the species <u>Archimedes</u>	168
21. Measurements taken on modified and lower densities of <u>Lichocyon</u> , <u>Pennsylv</u> , <u>Thalys</u> and <u>Troscus</u>	168
22. Measurements taken on <u>Irionys</u> cf. <u>harisi</u>	173
23. Measurements taken on <u>Irionys</u> cf. <u>harisi</u>	178
24. Measurements taken on <u>Lasiarchus</u> <u>caudatus</u>	188
25. Measurements taken on <u>Polydactylus</u> cf. <u>W. Jorda</u>	208

LIST OF FIGURES

Figure	Page
1. <u>Archaeobutyrus laevis</u>	13
2. <u>Archaeobutyrus laevis</u>	18
3. <u>Archaeobutyrus laevis</u>	22
4. <u>Archaeobutyrus laevis</u>	25
5. <u>Archaeobutyrus laevis</u>	27
6. <u>Archaeobutyrus laevis</u>	31
7. <u>Stenocratus pallasi</u>	38
8. <u>Stenocratus pallasi</u>	41
9. <u>Stenocratus pallasi</u>	45
10. <u>Archaeobutyrus laevis</u> on <u>Stenocratus</u>	48
11. <u>Stenocratus pallasi</u>	50
12. Diagram of the relationships of <u>Stenocratus pallasi</u>	54
13. <u>Archaeobutyrus laevis</u> and <u>Archidona Floridae</u>	100
14. <u>Archidona quadris</u> and <u>Archidona cf. quadris</u>	110
15. <u>Archidona quadris</u>	114
16. <u>Archidona quadris</u> , <u>Archidona</u> sp. A, and <u>Archidona</u> sp. B	118
17. <u>Archidona quadris</u>	119
18. <u>Archidona quadris</u>	119
19. Left ventral view of <u>Archidona quadris</u>	119
20. <u>Archidona quadris</u>	120
21. <u>Archidona quadris</u> and <u>Archidona quadris</u>	122

LIST OF FIGURES (CONT.)

Figure	Page
21. <i>Thalys</i> sp., <i>Thysanus</i> sp., and cf. <i>Leucostomus</i> sp.	118
22. <i>Thysanus</i> sp.	142
23. Cladogram of proposed relationships within the Protoselidae	152
24. χ^2 of <i>Leucostomus</i> and <i>Thysanus</i>	168
25. Epistome of <i>Thysanus</i>	178
27. Epistome of <i>Thysanus</i>	178
28. Epistome of <i>Leucostomus</i>	177
29. Histogram of H_1 length in samples of <i>Leucostomus</i>	184
30. Histogram of H_2 - H_3 length in samples of <i>Thysanus</i>	184
31. Proportions of mesodorsal, flammulae sp., and flammulae near H_1 length	184
32. <i>Leucostomus</i> <i>Leucostomus</i>	188
33. <i>Leucostomus</i> (mesodorsal) sp.	188

ABBREVIATIONS

AMNH	American Museum of Natural History
FMNH	Frick American Museum, AMNH, New York City
USNM	U. S. National Museum of Science, University of Bologna, Rome
TSM	Timberline Research Organization, Lake Wales, Florida
UCP	University of California Museum of Paleontology, Berkeley
USF	Florida State Museum, University of Florida, Gainesville
USNM	National Museum of Natural History, Washington, D.C.

n	number of specimens
\bar{x}	mean (\pm standard error)
s_x	standard error
O.R.	observed range
CV	coefficient of variation
t	Student's t value
P	probability value
l	length
w	width

All measurements are in millimeters. Measurements in parentheses are approximate measurements.

Dissertation of Dissertation Presented to the Graduate Council
of the University of Florida in Partial Fulfillment of
the Requirements for the Degree of Doctor of Philosophy

CARNIVORA FROM THE LATE OLIGOCENE/LATE Eocene BORE HILLS,
ALABAMA COUNTY, ALABAMA

By

Don Alan Jacobs

March 1988

Directed by: S. David Webb

Major Department: Zoology

Eleven taxa of Carnivora are described from the latest
Oligocene (Late Eocene) Leno Lake Bed Local Fauna, Etowah
County, Florida. Two new genera of Procyonidae, Archonotus
and Paranotus, are described. Descriptions are given for the
new carnivoran species Archonotus leno (Oligocene),
Paranotus gallus (Oligocene), Archonotus clausen (Procyonidae),
Paranotus leno (Procyonidae), and Archonotus leno
(Procyonidae). In addition with the descriptions of the two
new procyonids from the Leno site and a review of the Procyonidae,
twelve additional procyonid taxa are described from HockingFossil
(early Eocene) to HockingFossil (early Eocene) deposits of western
North America and Florida. New taxa that are described include:
Archonotus leno, new species, Archonotus gallus, new species,
Archonotus clausen, new species, Archonotus leno, new species,
and Archonotus leno, new genus and species.

The genus Archiprionotus is placed in the Stenotritidae, a family characterized by a specialized dentition and by a primitive lacrymosinus, lacking a septum bullos. The stenotritids are not assigned to the Felidae. Archiprionotus is a member of the subfamily Heterophenacinae, which also includes Protophacops, Amphisternon, and Stenotritus. Stenotritus, a true felid, possesses a septum bullos and is derived from a North American species of Protophacops.

The earliest known occurrences (Cret. Amphiliinae) of Procyon and Basile are documented. A cladistic analysis of the Procyoninae demonstrates that the new genus Procyon is the primitive sister taxon of Procyon and Basile. The new genus Archoprocyon is probably most closely related to the late Tertiary Procyon group of South American procyonines. The primitive sister group of the higher Procyoninae discussed in this paper includes Archoprocyon and the European Eudipylina (early Miocene) genus Eudipylus.

The paratype species of Archiprionotus, Archiprionotus ferox, is demonstrated to be a member of the Archiprionotus brevirostris species group. The generic name Archiprionotus is restricted to members of the Archiprionotus group. The generic name Archiprionotus has priority for the taxa that are included in the Archiprionotus brevirostris species group. Two taxa of Archiprionotus, Archiprionotus cf. ferox and Archiprionotus cf. brevirostris, are recognized from the Lower Eocene and Tertiary faunas.

INTRODUCTION

The Love Bone Bed was discovered in 1934 by Mr. Don Love while sitting on pine crop on his land near Archer, Florida. Reid, Reelfoot and Reelfoot (1980) present a detailed study of the geographic and geological setting, stratigraphy, biohermeneutics, biostratigraphy and paleontology of the site and its vertebrate fauna. Here a brief summary is presented here. The Love Bone Bed consists of fluvial sediments of the Bladen Formation that fill a complex stream channel deposit cut into the underlying limestone of the late Eocene Crystal River Formation. The fluvial sediments represent a single depositional cycle and fine upward from coarse psammatic sands and gravels to orange clay sands. The age of the Love Bone Bed local fauna is latest Oligocene as indicated by the stage of evolution of several mammalian taxa, such as the species of *Barboricichthys*, *Isotomus* and *Paratimarchus* described below. Early Neogene fish taxa such as ground sloths and beavers are conspicuously absent in the Love Bone Bed local fauna.

The Love Bone Bed local fauna is remarkable for its wealth of carnivore material. Carnivores are very poorly represented in Florida Neogene faunas. The Love Bone Bed provides the first detailed picture of the late Miocene Carnivores of eastern North America. Two of the more interesting taxa are the two new genera of *Procyonidae*, a family with a poor fossil record. In conclusion with the

description of the Long Bone Shed material, the location of the site and the unclassified material of non-descriptive prospects under its care available for study. This material is described below.

SYNOPSIS AND INTRODUCTION

Order Carabidae

Suborder Pylodinae

Elaphidion, Bartholomaeella and Elaphidion are subgeneric genera characteristic of the late Miocene of North America. Their recognition and taxonomic assignment have been sources of confusion in the literature. In this paper material from the latest Eocene/early late Oligocene, Alachua County, Florida is described and the systematics of these two genera are reinterpreted. Post-cranial material of Bartholomaeella and Elaphidion is described and compared in the section following the systematics of these two genera. A list of the postcranial material is given in Appendix 1.

Before cranial material was described and the genus Bartholomaeella created (Schultz, Schultz and Martin, 1975), members of this genus were variously assigned to Elaphidionellus, Elaphidion, Proelaphidion, and Elaphidionella. The first specimens of Elaphidion to be described and some subsequent material were placed in Proelaphidion (see synonymy in Martin and Schultz, 1974). Other material, initially described as a new species of Proelaphidion, became the paratype material of Elaphidion (Otte, 1964) and an ancestor-descendant relationship with the Oligocene genus Elaphidion was suggested. In this paper

Rhynchodonta, Barbouroffilia, and certain other genera are removed from the Felidae and placed in the Eumetridae, a name proposed by Cope (1889), long abandoned, but here reconstituted into what is intended to be a vertical group. The Eumetridae are characterized by a primitive barboninean lacking a septum bulbus and by dental specialization which prevent this family from being associated to the Felidae. Barbouroffilia, on the other hand, is a member of the Felidae, derived from a North American species of Proaenictes.

Family Eumetridae

General diagnosis. Cat-like carnivores with the following primitive carnivoran characteristics: septum bulbus absent, postglenoid foramen and ellipsoidal canal present, and posterior prearticular foramina opening on the maxilla, the following felid characters: retractile claws and loss of M_2^3 , and the following eumetrid characters: P^3 absent, M_2 reduced to absent, incisors vertical, lacking accessory lobes, P_3 , P_4 and P^3 without posterior cuspules, molar process well developed, paracristal process reduced, and maxilla with at least a slight flange.

Discussion. Turner (1948) was the first to recognize the importance of the structure of the maxillary barbonineus as a taxonomic trait, especially for the Canivores. The usefulness of maxillary characters in interpreting faunal relationships within the Canivores has since been confirmed by many workers (e.g. Flower, 1953; Smith, 1955, 1963; Ford, 1974, 1977; Telford, 1976). Cope (1889) was the first to note differences in the rat

regions of Asia that are classified as Felidae and established the family Blarinae for those genera with "caniniform and caniniform fangs" entirely distinct from the fangs; incisors posterior, an affodentoid canal, and postglenoid and postorbital foramina" (p. 408). He was unable to determine whether any of the taxa he included in the Blarinae possess a certain buffer. Cape noted that his higher Blarinae were dentally too specialized to be associated to the Felidae. He hypothesized that this subfamily was derived from *Proailurus* through *Panthera*. He considered that these two genera might be primitive Felidae. He derived *Prailurus* and *Lailurus* from *Hylophonus*, making his Felidae a polyphyletic group.

Reith (1960) rejected this classification and divided the Felidae into two subfamilies: the Machelodontinae, the saber-toothed cats, which he derived from *Hylophonus* and *Lailurus*; and the Felinae, derived from *Blarina* and *Prailurus*. This classification has been followed by most American workers, although Simpson (1945) retained a subfamily Blarinae for those taxa considered to be related to the ancestry of the Felidae. He also recognized *Proailurus* for "an unspecialized, in part structurally ancestral, offshoot of the earliest Felids" (p. 280).

Flower (1961) followed Cape (1958) and Teilhard de Chardin (1961) in dividing the Felidae into two groups: Blarinae, saber-toothed with a primitive dentition, and Felinae, caniniform with a *Lailurus*- or *Prailurus*-like dentition. There are saber-toothed and normal catlike groups in both subfamilies. Brown (1967) made a detailed comparison of skull material and dental morphology of

Belontiidae and Poeciliidae. He noted the many similarities between these two genera and concluded that they should be classified together in the same subfamily, the Alburninae of Probst, and should not be split apart as in the classification of Matthew, Shannon, or Hough.

A major problem in Probst's (1961) classification is that his Alburninae is a horizontal group characterized by shared primitive characters, such as presence of an epilophoid caudal. Shared primitive characters can be used to define a paraphyletic taxon if this taxon is also characterized by certain shared derived characters and is not based on convergent or parallel characters. The latter is true of Probst's Alburninae, as well as for the other classifications. They are composed of polyphyletic taxa. Issacoff (1981a) recognized that the felidae were composed of two distinct groups: the Alburninae (Alburnidae and Poeciliidae) and Hoplophorinae (Hoplophorinae, Amnirostridae, and Amniidae) on one hand and the Amnirostrinae and its descendants, the felidae and Macrinodontinae, on the other. He considered recognizing these two groups as separate, vertical families, but declined to do so because of what he considered uncertainties in the fossil record. The Alburnidae is here recognized and composed of Issacoff's Alburninae and Hoplophorinae.

A character of critical importance in feliform classification is the apical belton (Issacoff, 1981). A bilobate apical belton is a derived character having the felidae, Alburnidae, and perhaps the Amnirostridae. The apical belton is usually interpreted as being unilobate, but the exact homologies of the bones composing it are unknown and it may in fact be bilobate (J. Reel, 1974, pers. comm.)

or perhaps a subbasal septum may be primitive for these three families. The absence of a septum bulge is primitive for the Cuvieriidae. Rought (1950) noted that a septum bulge is absent in the Aliveriidae. Branstetter (1964a) and most others have agreed with Rought's findings. I could find no trace of a septum bulge, including related characters such as a raised ridge on the promontory, in the Aliveriids in the collections of the BMNH and the USNM. Clark and Samsbury (1972), however, have claimed that *Aliveria* and *Hoplaphysina* possess septum bulge. Branstetter (1967) has noted the presence of a septum in each of these two genera alone, but demonstrated that it corresponds in position to that of caudo. I noted this feature in a few of the better-preserved *Aliveriidae* shells. As noted below, *Hoplaphysina* also possesses a caudo-like septum, which is interpreted here as being primitive for the Cuvieriidae.

An important difference between the Aliveriidae and Hoplophysinidae is the presence of a parastyle on the P^1 in species of the latter. A parastyle is a diagnostic character of the Pylaeidae. This raises the possibility that the Hoplophysinidae are placed in the Aliveriidae on the basis of shared primitive characters: a parastyle has evolved independently in the caudo subfamily Hoplophysinae, in the Procyonidae, and in the Pylaeidae. Even the similarities between *Hoplaphysina* and *Aliveria* pointed out by Branstetter (1967), if probably evolved independently in the Hoplophysinidae as well. This then raises the problem of the taxonomic placement of the Aliveriidae, if characters such as P^1 with a parastyle and a septum bulge are derived features uniting the Aliveriidae, Squalidae, and Pylaeidae. This means that these three families share a common ancestor that should be classified

distinctly as a starfish. Cope (1885) was the first to note that the starfishes are definitely too specialized to be ancestral to the Felidae. The evolution of a cat-like habitus has evolved independently in many lines of carnivoran mammals besides the Felidae and Canidae. Examples include Saghuonops, an Eocene amphicyonid; Cynictaria, the Neogene viverrid; Ambelodon, the other-included Eocene creodont; and Dylacynops, the apicom of saber-toothed adaptation, a mesonid from the Eocene of North America.

The P^4 of the starfishes and the basicranial structure of the starfishes are cat-like. Bough (1953) established the superfamily Cani-Felidae for the Canidae and Felidae because of the cat-like structure of the basicranium of Canis. These characters are probably primitive for the Carnivora. Dental reduction associated with hyper-carnivorous/hisdon and development of retractile claws are characters which should place the starfishes in the Feliformia.

Subfamily Amphicyoninae

Dental diagnosis. Mandible with well developed symphyseal flange, upper canine elongate, laterally compressed and pruned, lower canine taurodontic, P_2 absent, P_3 reduced to absent, P_4 inclined posteriorly with collapsed anterior and posterior accessory cusps; P_5 absent, P^4 with straight and reduced protuberance.

Classification. Stolley (1971) divided the felidae into two subfamilies, starfishes and felines. The only members of the starfishes that he listed were members of his tribe Canini (Amphicyoninae), which included amphicyon, Canis, Canis, Canis, and Canis. Canis lacks the characters diagnostic of

the myliobatiform and should be included in the Monacidae. He later (1978) added a new genus, Spiracanthus, from the Heterodontidae of Libya, to his family. Spiracanthus is known from a mandible with a tooth for the incisors, median and P_3 and with P_4 and P_5 broken off nearly at the roots. Ginsburg (1978) concluded that Spiracanthus was closely related to European Sansanacanthus, but a little more primitive. Ginsburg stated that in Spiracanthus the P_4 had a fourth lobe and that the P_5 lacked a lobelet. These characters relate Spiracanthus and Sansanacanthus. However, it is difficult to see these characters, at least in the illustrations of these broken teeth. The small incisors, large P_3 , and relatively weakly developed apical flange support instead that Spiracanthus is closely related to Elacids, especially to derived forms such as Elacids affinis from the early Arkenian of North America, which have lost the P_5 and have a stronger flange than that of typical Elacids (Reedman, 1976). Sansanacanthus appears to be most closely related to Aplocheilichthys. Ginsburg (1958, 1964) discussed the derived characters shared by Sansanacanthus, Aplocheilichthys and Apollonia and noted that Apollonia is too specialized to be ancestral to Sansanacanthus.

Genus Aplocheilichthys Schultze, Schultze and Martin

Aplocheilichthys (rank n.) sp.

Table 1, 2, Figs. 1-8

holotype: VP 34437, juvenile skull (partially crushed and restored) with right i^{1+2} , left i^1 , dentition damaged with left c^1 missing and right and left r^2 .

Table 1. Measurements taken on *Agrostoides laevis*.

	N	T	S.E.	CV
F^2 length	8	8.30±0.38	8.2-11.2	18.0
width	8	5.30±0.17	4.8-6.8	8.4
F^4 length	4	40.40	42.1-49.8	
width	4	12.43	11.5-13.5	
F_3 length	4	5.35	4.6-6.5	
width	4	4.56	4.1-4.9	
F_4 length	15	29.00±0.89	18.5-27.6	5.5
width	15	8.04±0.14	7.0-8.5	8.6
F_1 length	25	36.70±0.29	29.0-35.7	4.6
width	25	16.74±0.10	11.4-15.7	9.2

Specimens. USNM nos. 24447, shell, holotype, 25071, 25072, P^1 , 25073-Holts, P^2 , 25074-25078, P^4 , 25079-25082, P_{2-3} , 25083-25084, P_{2-3} , 25085-25087, 25088-25089, R_1 , 25090-25093, P_4 - R_1 , 25448, 25449, right dentary with P_4 , R_1 ; 25450, right dentary with R_1 , 25451-25458, 25459, 25460, 25461, 25462, 25463, 25464, 25465, sublabial dentary fragments; 25466, mandible with P_{2-3} , C_1 , P_4 , R_1 , and P_{2-4} , R_1 ; 25467, mandible with P_{2-3} , C_1 , P_{2-4} , R_1 , P_{2-3} , R_1 ; 25468, left premaxilla and maxilla; 25469, 25470-25472, cranial fragments; all from the Lane Bone Bed, Alachua County, Florida, Tuleen Clarendonian Land Mammal Age.

Significance. Bared for Run and Hot Lane. In recognition of their Tuleen and others for the fossils of the Lane Bone Bed, especially Barbouriella.

Referred material. USNM nos. 25076, P^1 , 25112, P^1 , from the Black Rock Ranch local fauna, Green Valley Formation, Contra Costa County, California, Tule Clarendonian Land Mammal Age. BMNH no. 35-4-118, left mandibular fragment with P_4 and R_1 from the Smalls local fauna, Spillville Group, Ellis County, Oklahoma, early Neophilian Land Mammal Age.

Diagnosis. A species of Barbouriella intermediate in size between B. fricki and B. parvum. Clamps set as well developed and P^2 set as reduced as in B. fricki. P^2 more reduced and suboid process more extended than in B. parvum.

Description. The holotype (USNM 25447, Fig. 1) is the skull of a juvenile which still retains the deciduous dentition. The skull is badly damaged and much of the snout, palate, and suborbital region has been reconstructed. The reconstruction, especially the left side, is well preserved. The dorsal profile of the skull is much flatter

Figure 1. *Archaeosulcia* (level: 24437, holotype, lateral and ventral view (x 0.05).



than that of the skulls of the holotypes of Sarkowichella fricki and S. parvici (DeLuca, Schultz and Smith, 1990). This is caused partially by the reconstruction of the nasal region. However, juveniles Sarkowichella have a much flatter dorsal profile than do adults Sarkowichella (Morris and Stock, 1992) and this may also be true for Sarkowichella. In UF 21796, a posterior cranial region larger than that of the holotype, the sagittal crest is much better developed and appears to be relatively higher.

The upper incisors are uniserial and laterally compressed. The I^2 is slightly larger than I^1 . I^2 is larger than I^3 and has very fine serrations along its posterior edge.

The deciduous canine is smaller than the permanent canine. It has very weak internal and external grooves and anterior and posterior serrations. The permanent canine erupts rostrally to the milk canine (Fig. 18), apparently fully erupting before the deciduous tooth is lost, as is true for Sarkowichella (Morris and Stock, 1992). The permanent canine has a sloped root, weak internal and external grooves, and very fine anterior and posterior serrations. An interesting pathology occurs in UF 21811, a left premaxilla-maxilla fragment. The left canine has been lost and the bone in the region resorbed, indicating that the individual was able to survive for some time after the loss of at least one canine.

The P^3 is tricuspid, with the median cusp larger and taller than the anterior or posterior cusps. The tooth is single-rooted, or more usually has two fused roots. Maxilla fragment UF 21820 apparently had a double-rooted P^3 .

The P^A is extremely elongate and is the only functional upper cheek blade. There is no protocone. The metacone forms the longest blade. The plescone is the tallest cusp. The parastyle is very well developed. The ectoparastyle is very weakly to practically developed. A large root occupies the posterior two-thirds of the tooth beneath the metacone and posterior half of the plescone. Another root is beneath the anterior third of the tooth. A slender third root usually branches rostral to the anterior portion of the plescone, although in one specimen it is fused to the anterior root.

The lower incisors are unicuspidate and laterally compressed. Non-vertical wear facets indicate that they interlocked with the upper incisors. The incisors increase in size from I_1 to I_2 . The C_1 is similar in size to the I_2 . When present, the canine and probably all the molars have flat anterior and posterior surfaces. The M_2 is single-rooted and cortical. In most of the specimens there is a smaller posterior accessory cusp. The M_3 is not present in two of 18 specimens.

The P_1 has its cusps inclined posteriorly. The anterior accessory cusp is cortical. Its antero-internal ridge is serrated and in some specimens the ridge is enlarged to form a small cusplet. The main cusp is the largest and tallest cusp. It is laterally compressed and is finely serrated along its anterior crest. The posterior accessory cusp is laterally compressed and, together with the main cusp, forms a part of the lower shearing blade. A small posterior cusplet is developed on the posterior accessory cusp where it interlocks with the P_2 . This cusplet is not homologous to the posterior cuspulet of the talpid.

The P_1 is an elongate, thin, bill, blade-like tooth. The prebasal is longer than the paracord. The anterior sample of the prebasal is bent laterally forming a groove for the reception of the P_4 . The P_4 and P_5 function as a single blade, shearing against P^A . The coronal notch (Molnar, 1977, the slit at the base of the junction of the paracord and protoconid of P_5) is closed. The incisal (Molnar, 1977, the V-shaped cutting edge formed by the crests of the paracord and protoconid) is shallow. The scula of the P_1 meets with the scula of the paracord and overlaps of P^A . The scula, formed by the main and posterior accessory cusps of P_1 plus the anterior portion of paracord of P_1 , interlocks with the scula of P^A , composed of the parastyle and paracord.

The bulla is completely ossified (Fig. 1, 2). The nasal entoloparis forms a much greater portion of the bulla than does the ectoloparis. The ectoloparis is restricted by the enlarged mastoid process. The entoloparis appears to be U-shaped, forming the medial and lateral walls of the internal auditory meatus. The nasal entoloparis forms the medial, anterior, and apparently most of the ventral surface of the bulla. The bulla is flattened medially and posteriorly, and posteriorly forms a continuous flat surface with the mastoid process and occipital. There is no pre-ossified process. Medially the nasal entoloparis contains a lateral ridge of the basitragus. The basitragus is of 2440 forms a portion of the dorsal roof of the bulla, but it does not contact the petrosal. The median portion of the nasal entoloparis is expanded laterally and has a broad contact with the basiphosphor.

Figure 2. *Leptocottella borei*. W 2442, stereophotograph of left stic region (a 1-2). Abbreviations: C, posterior carotid foramen; L, posterior lacrimal foramen; N, rostral process; P, promontory of petrosal; R, rostral entotympanic; S, anterior crista.



There is no septum bullosa in any of the Florida scariel or in any of the skulls of *E. myrtil* examined at the AMNH. The preopercle is low and rounded, not high with a ridge where the septum bullosa contacts the preopercle as in *Tyllis*. A right otic region (cf. M422, Fig. 8) exhibits a probable rostral entopterygic, although it may be a broken fragment of the rostral entopterygic. Its location is appropriate for a rostral entopterygic (Quoy, 1934) at the junction of the tentaculophore, basiopterygial, aliopterygial and petrosal. It possesses a deep canal, presumably for the median branch of the lateral cartilage and terminates anteriorly at what is interpreted to be the anterior cartilage foramen. A crista in the wall of the rostral entopterygic extends to the rostral entopterygic. Posteriorly, the median entopterygic is also enclosed in a deep tube with a crista from the entopterygic extending from the posterior cartilage foramen anteriorly to the petrosal. These cristae can also be observed in *Phyllis*, a characteristically scarpiel skull from the middle part of the Ash Hillier formation. The cristae, especially the anterior one, seem to be homologous with the partial septum seen in the Scarpiel. A third crista is present laterally, along the canal for the facial nerve and the sigmoidotend artery, which runs from the facial canal to the sigmoidotend foramen.

The opiterygic recess is very deep, with a relatively well developed fossa for the greater tympanic muscle. The middle process is deeply recessed. The crista tympani is nearly circular and does not extend into the tympanic cavity.

The condylar and posterior lacrimal foramina are separate from each other, but lie within a common trough on the medial occipital surfaces of the skull behind the condyles. The posterior orbital foramen is at the most ventral portion of this trough. Dorsal to the posterior orbital foramen, is the posterior lacrimal foramen, is a smaller foramen which may be for the inferior temporal artery or alternatively for the proximal branch of the internal carotid. The foramen enters the bulla lateral to the opening for the median subocularid, which suggests it may have been for the proximal artery. There is no indication of any opening on the proximal end of a proximal foramen, although the higher facialis is well developed.

The maxilla process is greatly enlarged and extends below the level of the bulla. The stylomastoid foramen and hyoid foramen are medial to the maxilla process and are nearly on the ventral surface of the bulla. The maxilla and postglenoid processes are close together and probably partially enclosed a cartilaginous auditory tube. The external auditory meatus is more like that of *Gerrhina* than *Hylinx* (i.e., the ectotympanic is thick, separating the internal and external meatus). There is no postglenoid foramen. Between the glenoid process and the pharyngotympanic tube are small foramina, probably for the external tympanic artery and the chordotympanic nerve. The aliform canal is well developed but is relatively shorter than that of *Gerrhina*. Its anterior and posterior openings are no depressions containing the *f. rotunda* and *f. ovale*, respectively, but the openings are separated from these foramina

The size and shape of the mandible and its flange have been used in the diagnosis of the species of *Laricynotia* [Schultz, Schultz and Martin, 1976]. The large sample of mandibles at the lower size indicates that there is considerable ontogenetic and sexually sexual variation in the morphology of the rostrum (Figs. 3-4). Figure 3A is of a kinesis with a slightly worn R_1 . The jaw is extremely short and the flange is only incipiently developed. Its lateral surface is convex, not concave. In a juvenile specimen with the permanent lower canine erupting (Fig. 3B) the flange has begun to develop. The ridge marking the anterior boundary is very poorly developed and the ventral ridge weakly developed. The lateral surface of the flange is only slightly concave. In a young adult (Fig. 3C) the flange has become U-shaped with a strong ridge at its edge. The lateral surface is moderately concave for reception of the upper canine. In an old adult (Fig. 4B) the jaw is larger, with a deeper, more concave flange. The anterior ridge is strongly developed and extends anterior to the symphysis.

McTiernan [1977] has described rotation of the carnassial teeth in the Insectivora, especially in *Blarina*. In the tooth wear the upper carnassials rotate apically in order to maintain contact with the lower carnassials. In *Blarina*, since the symphysis is fused and lateral motion is limited, carnassial rotation is needed to maintain a scissors-like contact. In *Laricynotia* the lower carnassial rotates laterally along the anterior-posterior axis of the tooth. This lateral rotation of the R_1 (and also of the R_2 , but probably to a lesser degree) can be seen in the comparison of

Figure 3. *Indocalamus longi*. (A) W 25864, right mandible, external view ($\times 0.26$); (B) W 24427, left mandible, external view ($\times 0.26$).



A



B

Figure 4. Backbone is level. Left: modified, external class (a B.TK). (A) of 2019, (D) of 2019.



A



B

Figure 5. *Enchytraeus* ~~terre~~. Left mandibles, dorsal view.
Ln 0.781. (A) WF 24410, (B) WF 24428.



A



B

Figure 4. *Brachycephalus longi*. Composite sketches of four adult ventrals aligned at anterior axilla and dorsal margin.



a mandible of a young adult (Figs. 44, 45) with that of an old adult (Figs. 46, 48). In very worn teeth, the shear surface is nearly perpendicular to the roots and the dentine is worn away, exposing the pulp cavity. The symphysis is not fused in *Burgwerfella*, but its extreme length and the contact of the external flange with the enlarged canines probably limited lateral motion, which resulted in the development of coronoidal rotation to maintain coronoidal wear.

Comparisons and discussion. *Burgwerfella linei* is intermediate in size and morphology between *B. parvius* and *B. friedi*. Other material that is assignable to *B. linei* is from the late Black Rock Ranch local fauna of California (Kobayashi, 1944a) and the early Amphibian faunas local faunas of Oklahoma (Pitts, 1952). The Black Rock Ranch material, referred to the Pachyrhynchosaurs, includes an R_1 and a broken P^4 , described as P^3 and P^4 . The small material, referred to *Albanosaurus*? sp., consists of a left mandibular fragment with P_1 and R_1 .

Schultz et al. (1959) differentiated the early Cretaceous *Burgwerfella robusta* from the Eocene formation of California (Perran, 1938) from *B. whitfordi* from the lower Ash Hollow formation of Nebraska (Barbour and Cook, 1915) principally on the size and shape of the roots and flange. They and Gregory (1952) postulated that the difference might be a result of intraspecific variation, but in the absence of a large sample designed to compare the two, Schultz et al. (1959) attributed the possible specific difference to

geographic isolation. However, the mandible assigned to Harpagornis shaffneri from the lower Ash Hollow Formation of South Dakota is more similar to the denture of E. robustus than to that of E. whitfordi (Gregory, 1942). This variation is well within the limits of that of a single quarry sample, as is shown above for E. laevi (Fig. 4), and can be accounted for by age, sex, and individual variation. Greater variation can be seen in the sample of E. serrisi, from the middle Ash Hollow Formation of Nebraska, in the F-M collection. In contrast to the large variation in the mandible, the teeth show the limited variation expected within a species. The sample of E. laevi is highly significantly different in size from the sample of teeth of E. serrisi (Tables 1, 2). Harpagornis robustus is slightly smaller than E. serrisi. The three specimens above referred to E. robustus plus three specimens of E. serrisi from the Clarendon local fauna are significantly smaller than E. serrisi (Table 2).

Gregory (1942), Kells (1962), and Schultz et al. (1969) have pointed out the strong resemblance between Harpagornis and Antarctopelta. Pritchard (1961) pointed out that Antarctopelta, Harpagornis, and Pyralia share many derived characters. Gregory (1942) placed Harpagornis and Antarctopelta in the tribe Harpagornisini and suggested that the material briefly described by Sough (1933) from the Ash Hollow Formation might also belong in the Harpagornisini. This material was later to become the types of E. serrisi and E. fricki. Antarctopelta pringi, from the early Eocene of France (Ginsburg, 1961a), differs from Harpagornis in its smaller size, double-rooted P_3 with prominent anterior and posterior accessory

Table 2: Comparison of \hat{N}_T length in *Barbus rubiculus* stratified, *B. merulin*, and *B. longi*. See text for discussion of Student's t value (t_0) and probability value (p_0).

	<i>B. rubiculus</i>	<i>B. merulin</i>	<i>B. longi</i>
\bar{X}	25.26±9.475	26.37±9.499	26.19±9.254
S.E.	11.3-26.1	21.1-26.1	19.3-26.1
CV	3.1	8.3	4.6
n	4	5	21
t_0	3.95	10.37	
p_0	<.01	<.001	

coxae, P_3 with large columnar anterior accessory coxa, P_4 with conical coxa, P^3 with double roots, P^4 relatively low crossed with weakly developed parastyle, and shell without postorbital carapace. (A skull of *E. galileus* is figured in Patterson (1910) as *Archaeocetes galileus*.) The holotype of the two genera are very similar. *Archaeocetes* differs from *Archaeocetes* in possession of primitive characters that are modified with increasing size and diversification and increase in size of various... The two generally share the following derived characters: coxae with internal and external grooves, P^3 with an enlarged parastyle and well developed parastyle and lacking a protopod, P_3 with anterior coxite, P_4 without anterior and postglanoid furrows closed, as well as the characters diagnostic of the Haptophyceae.

Willard and Crawford (1940) described material from the Quaternary, Tertiary, and Quaternary, which they assigned to *Archaeocetes*. The holotype material of *E. galileus* is from the late Tertiary La Grise St. Alban fauna of France (Pittet, 1904). Mayall (1940) and most subsequent authors including Chubb (1961) have included *Archaeocetes* in *Archaeocetes*. The monotypic material is poorly known and it is uncertain whether the Tertiary material is conspecific with it, although it does strongly resemble the material illustrated by Rueda (1904). *Archaeocetes* described from Tertiary-Tertiary is larger than *E. galileus*, has a reduced anterior lobe on P_3 and P_4 , a fused double-rooted P_3 , P_4 with a possibly closed conical coxa (it is open in Rueda's illustration of the holotype material), and P^4 with an enlarged parastyle. The

material from the *Spizella*, mainly isolated teeth, is very similar to that of *E. palmeri*, as has been noted by Schultz et al. (1960). A possible specific difference is the double or fused double-rooted P_3 in the Williams material. Better material of both are needed before more accurate diagnoses can be made. *Elanoides forsteri* is a suitable ancestor for *Elanoides forsteri*. Sibley (1961a) considered the differences between the two to be too small to be worthy of generic distinction. In turn, *Elanoides forsteri* is an early *Elanoides* assigned from Canada that is derived from a form very similar to *Elanoides forsteri*. Perhaps if better material of *Elanoides forsteri* becomes known, generic distinctions between these three genera will form a continuum and all material should be assigned to *Elanoides*.

Early *Elanoides*

Subfamily *Phalaropodinae*

Elanoides **SHAW**

Elanoides palmeri n. sp.

Table 3, Figs. 7-12

Diagnosis.— Of 2447, left dentary fragment with E_1 , P_1

Material.— Of nos. 24405-24447, 24720-24726, E^1 , 24727, left P^2 , 24728, right P^2 , 24729, right P^{2+3} , 24730, 24731, left P^3 , 24732, right P^3 , 24733, E_1 , 24734, 24737, right P_2 , 24738, 24740, left P_3 , 24741, left dentary fragment with P_3 , ascending ramus, 24742, holotype, 24743, left dentary fragment with P_3 , broken P_1 , 24744,

Table 3: Measurements taken on *Blaschkea gelida*.

	N	\bar{L}	$S.D.$	CV
C^1 length	11	24.22 ± 0.803	$21.3-27.3$	4.1
width	11	13.53 ± 0.401	$11.2-15.8$	11.3
P^1 length	2	18.45	$16.4-20.3$	
width	2	8.60	$6.3-10.8$	
P^2 length	4	26.43	$21.7-31.2$	
width	3	16.47	$16.3-17.6$	
P^3 length	1		7.8	
width	1		13.9	
P_3 length	1		15.2	
width	1		7.2	
P_4 length	2	23.31 ± 0.342	$21.6-25.2$	4.1
width	2	9.34 ± 0.204	$8.1-11.1$	7.2
P_5 length	10	26.77 ± 0.368	$24.6-28.8$	4.2
width	10	11.35 ± 0.305	$9.6-13.4$	6.7
P_2+P_1 length	12	41.40 ± 0.448	$37.4-45.4$	3.7

24464, edentulous left dentary fragments, 24465, right dentary fragment with P_1 , 24467, right anterior dentary fragment with P_2 , 24470, right dentary fragment with P_{3+4} , 24471, right dentary fragment with P_2 , P_3 , 24472-24475, edentulous right dentary fragments, 24476, left atic fragments, all from the Live Oak bed, Alachua County, Florida, latest Claibornian Land Mammal Age.

Etymology. Named for Henry Gilmore of the AMNH.

Diagnosis. Cheek teeth distinctly smaller but much larger in proportion to mandible than and alveolar relatively shorter than in *B. immodicus*. Accessory cusps of P_3 and P_4 not well developed. P^3 with well developed basined trigon between protocone, paracone and parastyle.

Description. The upper canine is curved, elongate, acute in cross-section, somewhat wider anteriorly. It is flattened and serrated along its anterior and posterior edges. In four specimens the anterior serration bifurcates proximally, forming a narrow V, somewhat more than halfway from the tip to the termination of the enamel. The lateral(?) serration continues to the gum line on 4 P4s. The ventral serration is much shorter.

The anterior accessory cusp of the P^3 is small and medial to the middle of the tooth. The tooth is expanded medial to the central and posterior accessory cusp. The posterior cingulum is well developed, forming a cusp.

The P^3 is slender with an elongate blade-like antecone. The parastyle is well developed. A small ectoparastyle is present on the antero-ventral corner of the tooth. There is a circular, basined trigon between the protocone, paracone and parastyle. There

Figure 7. Stenocides, yellow. UF 20472, 1cm P^{3-4} . (A) dorsal view, (B) internal view. UF 20473, right saddle fragment with P_{3-4} . (C) dorsal view, (D) internal view (All $\times 0.75$).



It is large, separate labial root beneath the preincisor. The P_1^1 is a small tooth with a flattened oval occlusal outline. It has two fused roots.

The lower incisors are small and crowded into a triangle, with I_2 posterior. The lower canine is oval in cross-section, relatively large, but not very tall. A vestigial P_2 is sometimes present.

The P_3 has a large, laterally compressed, symmetrical main cusp and small anterior and posterior accessory cusps. The posterior cingulum is weakly developed. The tooth is directed slightly posteriorly and is wider posteriorly.

The P_4 has a well developed anterior accessory cusp which is more separated from the main cusp than is the moderately developed posterior accessory cusp. The anterior cingulum possesses a small cingular cusp.

A small ectacanth is present on the P_4 , although in some specimens it is extremely reduced (Fig. 8). A very small talonid may also be present. The tooth is curved laterally, relatively linear medially, with protoacanth longer and taller than ectacanth. The ectacanth notch is a narrow notched slit laterally, and is more deeply excavated medially. The ectacanth notch widens with wear.

A left basioccipital fragment (Fig. 8A) and a left otic region (Fig. 8B) are referable to Kiamegaster yellowi. In both, the suture bulge is preserved, dividing the tympanic cavity into antitympanic and postotympanic chambers. The suture bulge extends medially

Figure 8. *Stenocranus calliope*. (A) BP 20481, left mandible fragment with M_1 , holotype, external view (x 8.75). (B) BP 20481, left M_1 , external view (x 8.75).

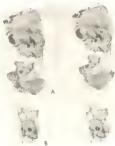


A



B

Figure 1. *Stenocratus galapagi*. *Stenocratus* (a 1/2). (A) UF 25555, left horizontal region, ventral view; (B) UF 24191, left otic region, ventral view. Abbreviations as in Figure 2 plus A, atriopleural canal; P, apical pleural process; I, internal auditory neuron; B, nauplius hollow; B, subventral hollow.



at an approximately 45° angle between vertical and horizontal. Hoyle (1932) distinguished between a horizontal pseudo-septum bulge of her *Archaeophlebotomus* and a vertical true septum bulge of her *Leptodus*. Bennett (1944) has noted that this difference is not important. The position of the septum bulge in the *Leptodus* is variable, depending on the size and shape of the bulge, sutured process, and glenoid process. The glenoid fossa is on the same level as the foramen oculi. There is no postglenoid foramen, but there is a shallow allapheoid canal. The condylar and posterior lacrimal foramina are not much more separate than in *Leptodus*. The maxilla and glenoid processes are not enlarged. The premaxilla is high and has transverse ridges along its crest. The ventral surface of the petrosal is more like that of *Leptodus* than that of *Leptodus*. In *Leptodus*, *Leptodus* and *Leptodus*, the internal auditory meatus is separated from the shallow epandicular fossa by a ridge not present in *Archaeophlebotomus*. In *Leptodus* and *Leptodus*, there is a squamous fossa, a depression formed as a posteromedial expansion of the petrosal around the aqueductus vestibuli, which is not present in *Leptodus* or *Archaeophlebotomus*. It is deeper in *Leptodus* than in *Leptodus*.

Leptodus. The maxilla of *Leptodus gillii* is somewhat larger in size than that of *Leptodus gillii* from the Cap Rock member of the Ash Hollow formation of Nebraska (Woodward, 1914). The cheek teeth are much larger, especially in relation to maxilla size. The maxilla of *L. gillii*, in contrast to *L. gillii*, has the bony skin, with an abrupt transition from the slightly convex buccal surface to the anterior and ventral borders

and has the ventral symphyseal extension diagnostic of *Stenocranius*. The nasosphenic fossa is smaller to that of *S. thomomys*; deep, but not deeply excavated under the dorsal and ventral rima, and without the rugose surface for muscle attachment as in *S. penicillatus*.

The mandible of *S. galli* is much smaller than that of *S. thomomys*, but the cheek teeth are only slightly smaller. The lower diastema is much shorter. The P^4 has a wider, more hooked trigon. The accessory cusps of the lower premolars are not as well developed and the anterior accessory cusp of P_4 is not as widely separated from the main cusp as in *S. thomomys*.

Discussion. Orita (1980) established the genus *Stenocranius* from *Parastachyris thomomys* (Reichardt, 1946) from the late Clarendonian Black Rock Ranch local fauna of California. He also referred material from the early Hemphillian Brewitt and Higgins local faunas of Oklahoma and the Paskapala of Texas to *S. thomomys*. *Stenocranius* is distinguished from North American *Parastachyris* in "the form of the 'lateral', the prominence of the accessory cusps on P_3 and P_4 , . . . the parastyle development on P^4 and on m^1 " (Orita, 1980, p. 275). Barker and Schultz (1978) pointed out that the holotype of *Reichsmodon schultzei* (Dodge, 1901), a mandibular symphysis which had not been reworked or illustrated until then, was not referable to *Reichsmodon* because it lacked an external flange, the incisor alveoli were small and crowded, and the canine alveolus was relatively large. They were able to work the symphysis with material assignable to *Stenocranius*. Matthew (1904) noted when

he made B. palmerensis a junior synonym of B. calaveras.

Reithrochilus palmerensis is the only valid specific name proposed to date for North American Reithrochilus.

Barth and Schaffa (1975) considered that Reithrochilus thomasi was probably a junior synonym of B. calaveras and used the name B. calaveras for material from the upper Ash Hollow Formation of Kansas and Nebraska. Depth of symphysis is probably the only significant measurement that can be taken on the holotype of B. calaveras. Neither of the mandibles from Black Rock Ranch possesses a symphysis, so there is no way that the symphysis of B. thomasi can be compared directly to the holotype of B. calaveras.

In characters other than the symphysis there is neither qualitative nor quantitative morphologic criteria to separate the Black Rock Ranch from the Amett material, thus the two should be considered conspecific. The larger samples (Figs. 10A-C) of Reithrochilus from the Love site and from Amett (including the sample from the AFSC Frack Laboratory Part of quarry Pit) indicate that there is a large amount of variation in mandible size within a single quarry sample. Ellis (1988) attributed the size difference in the two mandibles he described from Amett to a difference in age and possibly sex. Size differences in the Love site sample are probably primarily age-related, since some mandibles with worn teeth are relatively small. Likewise, the upper canines of B. pallasi apparently demonstrate sexual dimorphism (Figs. 10D, 11). Cheek teeth measurements, on the other hand, show much less variation [for the Amett sample (Table 4 for L_2 - L_4 length, Table 6 for symphyseal depth)].

Figure 18 Measurements taken on *Elanoides*. (A-C) Comparative measurements of *Elanoides gillett* (crosses), *Elanoides thomomys* from the Arnett local fauna (circles), *E. thomomys* from the Black Rock Ranch local fauna (squares), and the holotype of *Parahelorus peduncus* (triangles). (D) Lower canine length versus width of *Elanoides gillett*.

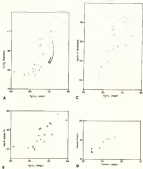


Figure 11. *Stegomyia albopicta*. Upper Canine (x 300). (A) of 26736, inset shows cross-section of tooth, (B) of 27085, inset shows magnified serrations.



The Ansett material has cyclophyll depths ranging from 41.7 to 43.8 (Fig. 1915). The holotype of *S. gillispayi*, with a depth of 50.7, falls easily within one standard deviation (5.82) of the mean (44.7) of this sample. However, this variable character does not provide sufficient reason to assume the two are conspecific. Although none of the new site specimens are as large as the Ansett specimens, two of the micromiles fall within two standard deviations from the Ansett mean of cyclophyll depth. If the exact locality of the holotype of *S. gillispayi* were known so that topotypic material could be collected, or if it could be reasonably demonstrated that there was only one species of *Elanoides* that included cyclophyll depths of 50.7, it would be reasonable to consider *S. thompsoni* a junior synonym of *S. gillispayi*. The holotype of *S. gillispayi* comes from the Republican River beds, Phillips County, Kansas. Republican River beds is an old name for the late Pliocene rocks of Kansas and southwestern Nebraska, usually members of the Spallina Group. In Phillips County rocks of Clauserian and Neophilian age are widespread (Griffard, 1943), rendering it probable that the locality will be rediscovered. Undescribed material in the Allen Frick Laboratory collections from the stratigraphic position of Kansas is larger than the Ansett or Black Rock Ranch material, although cyclophyll depths greatly overlap the Ansett sample and that of *S. gillispayi*. Because these problems are unlikely to be resolved, *S. gillispayi* is best considered a *sensu lato* and *S. thompsoni* should be applied to the other described material of *Elanoides* from the Flinn and the west.

Blattarispa evolved in North America from members of the *Pseudospha. latreidoides*-*Pseudosphaera polynesiensis* species group. This species group had been in North America since at least the Cretaceous. A cladogram showing relationships of these taxa is given in Fig. 3B. These taxa are united in the following synapomorphies (Denset point 1): heavy elytra, with sharp transition between anterior, lateral and ventral margin; elongate upper sternal, cheek teeth robust; and mesothoracic furrow deep and broad, especially ventrally. *Pseudosphaera polynesiensis* is the sister taxon to *Blattarispa* because they share the following synapomorphies (Denset point 2): increased size, better development of accessory cusps on the pronotum; relative enlargement of the P_{2+3} and lower fulcrum compressed into a triangle. *Blattarispa. latreidoides* and *B. pallens* share the following characters, which are diagnostic of *Blattarispa* (Denset point 3): mandible with internal flange, enlargement and separation of the anterior cusp of P_{2+3} ; stronger accessory cusps on P_3 , P^4 with reticulate and enlarged paraclytus, and upper sternal with double-serrated anterior ridge variably present.

Blattarispa makes its first appearance in the late Cretaceous and its last appearance at the end of the Mesozoic (Tiedford et al., in press). *Blattarispa* first appears in North America at the end of the early Mesozoic. Although these two genera have been confused in the past, both can be easily distinguished on mandibular and dental characters (Gardle and Schaller, 1988). *Blattarispa* has unrelaxed lower fulcrum, reduced lower cusp, B_1 with reticulate apex, mandible with internal flange and reduced coronoid process.

Figure 13. Cladogram of the relationships of Stenrodia giffard.



and I^B with reduced pretensions and enlarged ectoparasitism. **Phylotropy** is defined here (Larsson 1993a) as parasitism.

At the time of the migration of *Neotoma*, the Eurasian both the field *Microtus* and the vole-like *Microtus* became extinct in North America. Both *Microtus* and *Neotoma* occur in the early Neolithic and the local fauna of Tatars, but are from different quarters (S. Solovov, pers. comm.). A cause-effect relationship between this migration and the extinction is doubtful, but seems plausible at least in the case of *Microtus*. *Neotoma* and *Microtus* are similar-bodied cats, having cat-like limb proportions and probably hunted similar prey in a similar fashion. The extinction of *Microtus* may have been the result of competition with *Neotoma*.

The extinction of *Lophoceros* probably had a different cause. The dark-bodied animal was heavily built with short legs and powerful front quarters and, as further noted by Martin and Schultz (1955), seems to have been adapted to grazing on large, thick-stemmed acacias. They also note that the time of extinction of *Lophoceros* corresponds to the great drop in ungulate diversity at the middle of the Miocene with the widespread development of rangeland grasslands (Wink, 1977). The extinction of *Lophoceros* seems to be the result of climatic change which reduced the availability of prey species and which may also have reduced the cover it needed for defense or subduing prey.

Description of the postembryal material of
Barbouriella and Barroviella

Ellis. Barbouriella (Table 4) differs from Leleia and most other cirrarians, but resembles Spallanzania (Scott and Jensen, 1936) and Uroidea, in lacking star sockets. The anterior border of the transverse process contains the anterior articular process, forming a foramen connecting the sternal foramen, on the dorsal surface, with the anterior opening of the transverse foramen on the ventral surface. In Leleia there is a foramen transmitting a blood vessel from the anterior opening of the transverse foramen to the neural canal. In Barbouriella this foramen is extremely reduced in extent. The transverse processes extend well behind the posterior articulating surfaces for the axis and are pointed at their backwards extremities as in Leleia. They extend farther subaxial and their external margins are more curved than in Leleia. The dorsal surfaces are concave and contain numerous pits and scars of muscle attachments. The neural canal is relatively wider dorsomedially than in Leleia or Leleidia. The anterior margin of the neural arch is only slightly indented, even less than in Leleidia. Because of this the neural arch is proportionately long in the anteroposterior direction. The median tubercle on the dorsal surface is as prominent as in Leleia.

The Atlas of Barroviella is represented by one specimen with the transverse processes broken off. Star sockets are present. The sternal foramen has small anterior and lateral openings. In posterior view the maximum width and height of the neural canal are approximately equal. There is almost no indentation of the anterior margin

of the neural arch:-- the neural arch is wider transversely and narrower anteroposteriorly than in Fig. 10011a.

Fig. 10011b. The next complete axis of Archaeopteryx (Table 4) is from a young adult. The epiphysis is missing and the transverse processes and the anterior part of the neural spine are broken off. The neural spine is exceptionally high. The posterior portion is thin and narrow and projects well behind the posterior zygophyses. The crest line of the spine slopes anteriorly. Although the crest at the spine is broken, it does not appear to have extended as far anteriorly as in Fig. 11. The posterior border of the neural spine is broadly and deeply indented. The spine narrowed anteriorly above the posterior zygophyses so that in posterior view the axis is more similar to a thoracic vertebra than to a fetal axis. The anterior articulating surface with the atlas is directed more anteriorly than in Fig. 11. The bone covering the vertebral canal is short. The transverse processes are well developed and are more in the horizontal plane than Fig. 11a or Fig. 10011a. The posterior zygophyses are set in downward directed as in Fig. 11. The ventral surface of the centrum has a well developed median keel that widens posteriorly. On either side of the keel are two large deep depressions for the longus colli muscle, which may have been exceptionally well developed.

Fig. 10012. The axis of Archaeopteryx (Table 4) is short and stout. It is strongly constructed and differs from that of Fig. 11 in being wider transversely than long anteroposteriorly. The surface for attachment of the pedicle is much larger than would be expected for such a short axis. The surface extends relatively deep

Table 1. Measurements of *Peromyscus* atlas and atlas.

	N	\bar{x}	S.D.
ATLAS			
Greatest width across transverse process (breasted) width of anterior end across articulation for complex of skull	2	175.3	(160)-(190)
Breasted width across entire portion of articulation for atlas	3	61.59	59.1-65.2
Length from anterior end of articulation for complex to posterior end of articulation for atlas	1		66.2
Length of skull and along median line	4	63.73	60.3-67.5
Breasted length of transverse process, taken obliquely to face end of ends of scapulae	5	59.52	55.3-66.5
Breasted height from ventral condyle of inferior axis to dorsal surface of atlas	5	52.34	49.3-56.1
ATL			
Greatest width of posterior end of atlas (apex)	1		12.5
Length of condyle to tip of basilar process	5	47.39	44.3-51.6
Depth of ventral extended condyle to floor of neural canal and across posterior epiphysis	2		
Greatest transverse width across posterior epiphysis	3	31.74	29.8-35.2
Width across articulating surface for atlas	3	30.30	27.8-33.1
Width across transverse processes	1	55.64	50.3-61.6
Width across posterior condyles	1		(56)
Vertical distance from top of posterior end of atlas (apex) to bottom of posterior epiphysis	1		19.5

Table 3. Measurements of the corn-

	Antherostictis			Mormonula		
	N	\bar{x}	S.D.	N	\bar{x}	S.D.
Greatest length measured parallel to median line	4	47.27	62.3-73.0	2	101.26	93.9-108.2
Greatest width at anterior end and at other vertices for this	4	26.00	21.3-40.3	2	79.49	79.3-71.2
Greatest width of dorsal second vertebra	2	45.40	45.4-47.4	1		[20]
Greatest transverse processes	4	45.67	43.3-48.5	1		54.5
Greatest width between dorsal vertebrae of anterior symphyses	1		17.7	1		31.3
Greatest width posterior symphyses	4	17.73	16.4-19.4	2	15.90	32.3-24.4
Greatest depth of centers of first dorsal vertebra	4	54.40	51.3-60.3	1		31.5
Greatest distance from dorsal angle of anterior symphyses to ventral border of surface joining ilium	4	58.57	16.1-58.3	1		22.5
Width of corpus of third vertebra	3	8.00	6.3-9.3	1		12.3
Depth of centers of third vertebra	3			1		

ventrally and extends posteriorly onto the transverse process of the third sacral vertebra. The centers of the three sacral vertebrae decrease ventrally in size from first to third, with the third vertebra being even relatively smaller than that of *Spilotes*. The three neural spines are broad anteroposteriorly and are strongly developed. As in *Spilotes*, the spine of the first vertebra is vertical; that of the second, inclined somewhat posteriorly; and that of the third, decidedly posteriorly. The anterior zygopophyses vary in shape. Two specimens are longer dorsoventrally, two, anteroposteriorly; and one is subcircular. There is a process extending from the dorsal surface posterior to the anterior zygopophyses laterally around the zygopophyses to the anterior surface, as in *Scorpion*, *Diabaspis* and *Isanaspis*. The ventral articular processes between the first and second vertebrae are extremely well developed; those between the second and third only slightly less so. The dorsal sacral foramina are small. The ventral surface of the sacrum is relatively flat. In most of the specimens there is a slight keel on the third vertebra. The ventral sacral foramina are not large. The transverse processes are extremely flattened and are in approximately the same plane as the ventral surface of the vertebra. The posterior zygopophyses are extremely small. This and the small size of the posterior articular surface indicate that *Isanaspis* had a very short tail.

The sacrum of *Phacops* (Table 5) is long and slender. Sacral vertebra two and three are subequal in length and width to only slightly shorter anteroposteriorly than the first sacral vertebra.

The transverse processes are short. Those of the third sacral vertebra are exceptionally so. The surface for attachment of the pelves resembles that of *Reithrodon* and *Leiolagus*. It extends from just anterior of the second transverse process ventrally and then anteriorly. The dorsal sacral foramina are not enlarged. The anterior zygapophyses are only horizontally inclined than in *Leila* or *Leiolagus*. The neural spines are all broad anteroposteriorly. Dorsal spines one and two are more or less vertically inclined, neural spine three is inclined somewhat posteriorly. The posterior border of the third neural spine is located slightly anterior to the posterior zygapophyses, as in *Leila*. The ventral sacral foramina are relatively small, especially the posterior foramina. The ventral surface of the first sacral vertebra is flattened. The transverse processes extend at right angles to the long axis and curve only moderately ventrally at the lateral extremities. The ventral surfaces of the two posterior vertebrae are convex. The posterior zygapophyses and the posterior articular surface are moderately well developed but are smaller than in *P. jayak*, indicating that the tail was somewhat reduced.

Humerus.—The humerus of *Leiolagochelys* (Table 6) is short and massively built. It differs strikingly from that of *Leila*, especially in the development of the posterior, dorsal and lateral epicondylar ridges. These ridges are crown-like in degree of development. The posterior ridge extends along the distomedial surface nearly down to the distal end of the shaft. The deltoid ridge begins below the contact of the greater tuberosity and the

Table 6. Measurements of the larvae.

	n	Lengths, μ m		CV	n	Area, μ^2		CV
		\bar{x}	S.D.			\bar{x}	S.D.	
Brustak; length measured parallel to longitudinal axis	1		190					
Brustak; transverse diameter of proximal extremity	4	63.40	81.4-85.1					
Brustak; submicroscopical diameter of proximal extremity	4	70.50	76.8-85.2					
Brustak; diameter at middle of study extremities	2	66.50	65.5-67.5					
Brustak; width of distal extremity	2	92.45	92.1-92.8					
	16	74.20	66.8-74.2	4.3	4	75.0	66.8-80.0	
		92.670						
Least submicroscopical diameter of activating surface of stem	16	40.10	36.4-45.9	6.2	4	48.8	43.8-53.2	
		42.670						

based on the ventral border of the external surface. It continues across the external surface and joins the postoral ridge two-thirds of the way down the shaft. The area between the postoral and suboral ridges is slightly concave, largely because of the exceptional development of the latter. The shaft is flattened posteriorly and compressed transversely. As in *Leilidige*, the proximal end is narrower transversely than in *Ptilo*. The greater tuberosity also resembles that of *Leilidige* in extending further ventrally along the side of the head. The greater tuberosity does not extend as far internally, and the horizontal process is therefore very wide. Usually the lateral epicondylar ridge is broad, flattened and extends proximally more than one-third of the distance of the shaft. The entolepicondylar fovea is low on the humerus, just above the level of the trochlea, and is bordered by a thin epioleostylar ridge. The trochlea and capitulum are narrower and not as well developed as in *Ptilo*. Their external and lateral borders are more or less with the long axis. The medial epicondyle is somewhat dorsocentrally compressed. The olecranon fossa is deep, with well defined borders.

Only distal portions of the humeri of *Heterodige* (Table 4) have been recovered. These are similar in structure to *Ptilo* and *Leilidige*. The postoral ridge is better developed and appears to extend about two-thirds of the way down the shaft. The entolepicondylar fovea is less elongate and is bordered by a thicker and broader medial entolepicondylar ridge. The lateral epicondylar ridge is slightly broader and extends further distally. The suboral condyle extends further laterally but not as far ventrally. The olecranon

flexionation (Gonges, 1898), the angle the lateral border of the sternon fossa makes with the long axis, is about 30° . This is much larger than values reported by Gonges, but is smaller to that of the fossil *E. aggr.*

Ela. The size of *hypostachys* (Table 2) is very short and long. In lateral view the ventral surface is relatively straight, bending noticeably ventrally only at the distal end. The proximal surface of the sternon process resembles that of *Leptachis*. Distally there is a broad elongate median knob for the attachment of the mastic muscle. It is not elevated and there is no fossa lateral to this knob as in most *Lepta* and *Carya*. Ventrally the region for attachment of the triceps is broader than in *Lepta*. The mastic process, the proximal articular surface of the ventral notch, is more symmetrical and flatter than that of *Lepta*. There is much less expansion onto the external surface. Ventral and posterior to the proximal facet for articulation with the alve is an elongate depression. The median part of the shaft has an irregular diamond-shaped cross-section. There is a well developed median dorsal ridge and a strong internal ridge. The distal portion of the shaft is not as flattened transversely as in *Lepta*. The pliciform facet is small.

The size of *Stenostachis* (Table 2) resembles that of *Lepta dent.* In lateral view the ventral margin of the shaft is relatively straight as in *Leptachis*, but distally the stylod process is bent posteriorly as in *Lepta*. The proximal surface of the sternon is relatively narrow transversely. The two tubercles are separated by a well

Table 2. Measurements of the alga.

	Heteroceratids				Heteroceratids			
	n	\bar{x}	S.D.	CV	n	\bar{x}	S.D.	CV
Greatest length measured parallel to longitudinal axis	3	240.7	120-250		3		207	
Smallest width of posterior surface at alarveae								
provent	11	22.11±0.24	21.8-22.8	11.8	3	22.70±0.19	18.3-23.8	18.9
Greatest transverse width of proventer region cavity	16	32.36±0.501	21.9-35.0	8.9	3	34.50±0.535	30.3-37.7	17.1
Anteroposterior diameter across oesophageal process	16	52.36±0.108	48.8-57.1	7.3	3	47.25±1.166	44.3-54.8	17.1
Anteroposterior diameter of shaft at provent end of union tube	4	28.36	25.4-29.2		3	29.14	25.1-31.2	
Transverse diameter of shaft at provent end of union tube	3	18.55	17.4-21.4		3	18.56	15.4-23.6	
Greatest anteroposterior diameter at distal extremity	4	26.38	23.9-28.9		2	27.95	25.3-23.8	
Smallest width of distal extremity	3	19.43	18.0-20.8		2	18.80	15.3-18.5	

developed dorsomedial fossa. The external tuberosity is larger than and dorsal to the internal tuberosity. The internal tuberosity is better developed than in *E. gaga*. Sponer (1957) states that these two tuberosities are for attachment of the biceps brachii muscle, a large external tuberosity being indicative of a large median triceps. The acromial process is narrow transversely and extends only slightly onto the internal surface. The proximal radial facet is narrow, especially distally. The shaft is slender and is transversely compressed.

Radius. The radius of *Leptomastix* (Table 4) is considerably shorter, but relatively heavier, especially distally, than that of *E. gaga*. The shaft is more bowed. The long axis of the head is set at a greater angle to the long axis of the distal extremity than is that of *fallis*. The head of the radius is rounder than that of *fallis*, especially at the border that articulates with the ulna. The radial tuberosity, the site of insertion of the biceps tendon, is weakly developed. Opposite this, on the dorsal surface, is a pronounced knob for the attachment of the lateral collateral ligament. Distal to the radial tuberosity, the squared surface for the attachment of the abductor pollicis longus muscle is very well developed. The shaft widens and flattens distally. The distal articular surface is relatively large, especially dorsomedially. The articular surface is more concave than that of *fallis*. The styler process is saddle-shaped, with a large dorsal and a smaller ventral surface, and is proportionately much larger and more in line with the long axis of the radius than is *fallis*. The distal grooves for the tendons and muscles are well developed.

Table 3. Measurements of the rostrum.

	Lutjanus fulvus			Lutjanus		
	\bar{x}	\bar{s}	Δ_{95}	\bar{x}	\bar{s}	Δ_{95}
Length measured along ventral border	3	136.065.15	135-138	3	20.76	20.1-21.3
Longest diameter of greatest area	3	31.029.032	27.6-33.2	3	25.134.038	21.2-31.2
Greatest diameter taken at right angles to base	3	24.254.035	20.5-28.2	3	28.0342.039	23.4-33.8
Diameter at posterior end of snout at widest	3	23.895.036	21.8-25.8	3	26.233	22.7-27.8
Protrusion of snout at widest	3	51.042.018	51.8-51.8	3	18.00	13.3-25.8
Greatest snout at dorsal end (taken normal to lateral face)	3	47.7350.872	38.4-46.7	3	63.607.016	49.4-62.7
Greatest diameter of snout and	3	38.6760.693	33.3-43.8	3	29.347.003	25.2-38.2
						18.8

The radius of Therapsites (Table 8) is folio-lutea in its proportions. The radial tuberosity is smaller and lies more proximally than in folio. Proximo-distally to this is a prominent pit. The distal articular surface with the olea is rounded in outline.

Scapholagus. The scapholagus of hircoscolalia (Table 8) differs markedly from that of folio. The proximal surface for articulation with the radius is more concave. The concavity for the reception of the styloid process of the olea is broader and deeper, making the proximal surface wider on the radial side, especially dorsally. The radial-ulnar projection of the scapholagus is more tubercle than that of folio. It lacks the articulation for the sesamoid on its radial surface. On the distal surface are two facets for the trapezium. The palmar facet is much larger and has an elongate oval outline. The smaller facet is almost at right angles to the larger one and is connected to the trapezoid facet. The trapezoid facet is concave along the radial-ulnar axis and is wider radially. The facet for the sigmoid is sharply defined. The unctiform facet is more oval in outline, more concave, and is located more on the distal surface than that of folio.

The scapholagus of Therapsites (Table 8) resembles that of folio, especially folio. The articular surface for the radius extends somewhat farther onto the dorsal surface of the olea side than it does in folio. The concavity for the styloid process of the radius is better developed. The sesamoid facet is larger. The facet for the trapezium is concave and extends to the palmar border. The

Table 3. Measurements of the crabs.

	N	Antennae			Measurements		
		T	S-L	SL	T	S-L	SL
SCUDICARIDE							
Preblast, transverse diameter across normal eye							
normal	13	28.75±0.311	17.4-21.3	6.7	18	36.30±0.176	26.2-36.7
Preblast, dorso-lateral length	13	28.57±0.316	18.0-22.6	6.3	18	37.00±0.345	27.4-36.8
Preblast, postoculolateral diameter	13	25.45±0.417	16.7-21.6	6.7	8	26.94±0.359	19.3-22.7
THALASSIDROMA							
Preblast, dorso-lateral length	2	26.50	16.2-26.8				
Preblast, postoculolateral diameter	2	16.75	15.3-25.6				
Preblast, width of preblast surface	2	16.25	15.0-16.5				
MACOMA							
Preblast, dorso-lateral length	6	25.57±1.426	16.7-31.4	6.7	7	23.873	24.7-26.7
Preblast, postoculolateral diameter	6	16.24±0.371	10.2-19.2	6.4	7	20.4	15.9-25.7
BEUTOGAM							
Preblast, lateral diameter	2	26.25	18.3-31.6		7	27.1	27.4-31.2
Preblast, dorso-lateral diameter	2	26.56	26.3-30.3		7	23.56	21.8-24.1
Preblast, width across dorsal surface	2	17.46	17.1-18.1		7	16.3	17.7-18.6

facet for the scapula is not as concave and is straighter than that of Felis.

Trapezium. The trapezium of Lariscusfelis (Table 8) differs most from that of Felis in its articulation with the scapholunar. In Felis there is a broad facet covering the slightly concave proximal surface. In Lariscusfelis there are two distinct proximal surfaces at approximately right angles to one another. The ventral half, corresponding in position to the ventral surface of the trapezium in Felis, contains the major facet. It is internal-externally elongate and does not extend to the ventral border. The dorsal half of the proximal surface is concave externally. Laterally and internally is a facet that articulates with the smaller trapezium facet of the scapholunar. Laterally and internally is a presumably third facet that might articulate on the internal border of the trapezoid facet of the scapholunar. The dorsal surface is subequal in outline. On the outer surface the facet for metacarpal II is concave and contacts that of the trapezoid medially. The proximal border of the trapezoid facet is sharply concave, corresponding to the borders of the two smaller scapholunar facets. The facet for metacarpal I is more strongly curved both convex dorsally and concave ventrally than that of Felis.

Hamate. In Lariscusfelis (Table 8) the internal border of the proximal surface of the scapula is indented medially more than it is in Felis. The articular surface for metacarpal III is relatively small. The articular surface for the scapholunar is more curved and extends further ventrally and proximally and the ventral knob

is relatively small. These structures permit greater flexion of metacarpal III. On the internal side the proximal articular projection articulates with metacarpal III, metacarpal II, and the trapezoid, respectively, from proximal to distal. The ungiform facet is narrow in width. The proximal arm of this asymmetric U-shaped facet extends so far ventrally as does the distal arm. The ventral surface is at about the same level as the ventral border of the distal facet and is flatter than that of folia.

In Struthio (Table 4) the ungiform is folia-like. The articular surface for the sesamoid is broader transversely and continues further dorsally than it does in folia. The proximal surface forms a continuous convex curve from the dorsal to ventral border. The facet for the ungiform is broad dorsocentrally and has short, widely separated proximal and distal arms.

Equifolia. In external or internal view the ungiform of Equifolia (Table 5) is more rectangular than that of folia; that is, it is narrower proximally than it is dorsocentrally. The facet for the sesamoid is extremely convex dorsally and concave ventrally. The convex portion is longer and wider and extends into the distal surface. The distal facet for articulation with metacarpals II and V is suboval in outline and does not extend to the ventral border. On the proximal side of the ventral surface is a large knob that is not directed proximally as in Struthio or some folia. On the external surface the facet for the ungiform does not extend as far distally as it does in folia.

In Marrechia (Table 14) the facet for the isopodites is somewhat less convex than that of Fella. The dorsal border of this facet is wider and straighter. The condylar facet narrows at its distal border, not widening as in Fella.

Metapodials. The metapodials and metatarsals of Leptogriffis are easily distinguished from those of Fella. They are very robust with large proximal processes. The shafts are dorsoventrally compressed and the distal articular surfaces are flattened distally.

Metacarpal 1. Metacarpal 1 of Leptogriffis (Table 16) resembles that of Onchis, although it is relatively shorter and broader. The facet for the trapezium extends over the entire proximal surface. The facet is more elongate and deeper than that of Fella and is distinct from the dorsal surface proximally-ventrally. The distal end is only slightly offset from the long axis. The median lobe of the articulating surface is very weakly developed.

Metacarpal 1 of Marrechia (Table 10) is similar to that of Scyllaea and Pachirostris. It is relatively broader than is Fella and has a ridge of the dorsal surface. The proximal surface is relatively flat, without the sharp break between the articular and non-articular surface present in Fella. Proximally the facet for articulation with the trapezium is narrower dorsoventrally than the non-articular surface and forms a spicula on the inner surface, as in Scyllaea and Pachirostris. The distal end resembles that for Onchis, with its longer, notched articulating surface that does not extend onto the dorsal surface. The median lobe is less well developed than in Fella, in contrast to Scyllaea and Pachirostris, in which it is better developed.

Table 18. Measurements of metacarpal 1.

	N	Permanentials		Dx	S	T	Electrons	
		I	S.S.				S.S.	CF
Constant length normal to proximal end	5	25.44±5.432	25.3-32.4	2.3	3	39.40	25.3-37.3	
Constant width of proximal end	5	13.20±5.584	12.1-19.6	4.4	3	22.50	21.1-25.9	
Transverse width of distal articulating surface . . .	5	14.30±5.124	11.3-18.9	5.4	3	17.40	16.2-18.3	

Metacarpal II - In Surigonesella (Table III) the proximal surface for articulation with the trapezoid is slightly convex, except for the dorso-lateral corner, which is elevated, forming a concavity between it and the rest of the proximal surface. The process for the attachment of the interosseous muscle is large and gives the proximal surface a broad ventral border. The dorsal surface lacks the groove for the radial artery, which is present in Fig. 10. On the articular surface the dorsal facet for metacarpal III is more concave and elongate than in Fig. 10. The ventral facet for metacarpal III faces more anteriorly and is therefore at an oblique angle to the ventral sagittal facet, set at acute angle as in Fig. 11. The ventral sagittal facet is relatively smaller and does not occupy all of the proximovertral surface. An oblique line separates this facet from an enlarged area for connection of the interosseous muscle that contacts the proximal surface. On the lateral surface the trapezoid facet is weakly convex. The distal articulating surface is slightly asymmetrical, with subequal external and internal surfaces.

Metacarpal II of Stenocratus (Table IV) is similar to that of Fig. 10. The facet for the trapezoid is not as wide and the dorsal facet for metacarpal III is more concave and extends further proximally. Metacarpal II of Microdactylus or Fig. 12 is more slender than that of Stenocratus. In all three genera the proximal surface is slightly convex and the distal surface asymmetrical.

Metacarpal III - In Stenocratus (Table IV) the proximal facet for articulation with the trapezoid is distinctly proximovertrally convex.

Table 11. Measurements (P, 25%, 50%, 75% of notochordals II-IV of *Archaeopteryx*

	P	25	50	75	N
Greatest length	16.71-16.101, 18.7-20.3, 11	16.20-1.362, 27.3-27.8, 11	15.31-16.533, 40.3-40.8, 11	15.55-16.819, 40.1-40.6, 11	
Greatest anteroposterior diameter at greatest end	13.47-16.133, 19.1-19.6, 11	21.03-21.595, 17.4-22.1, 11	11.57-16.577, 16.4-16.8, 11	12.13-16.284, 16.5-16.8, 11	
Greatest dorsoventral diameter of process and	20.47-21.123, 18.3-21.2, 11	21.27-21.182, 18.4-21.5, 11	21.27-21.277, 19.5-21.5, 11	18.13-18.186, 18.4-21.5, 11	
Transverse diameter at middle of shaft	12.13-16.125, 18.4-21.6, 11	16.46-16.385, 18.4-21.7, 11	11.41-16.126, 18.7-19.8, 11	11.33-16.124, 18.7-19.8, 11	
Anteroposterior diameter at middle of shaft	2.45-16.136, 18.4-21.5, 11	9.54-16.285, 18.4-21.5, 11	16.13-16.241, 18.4-19.8, 11	1.55-16.284, 18.4-19.8, 11	
Greatest anteroposterior diameter at distal end of shaft	12.23-16.123, 16.3-18.2, 11	18.59-16.285, 18.4-21.5, 11	12.13-16.283, 18.4-20.7, 11	18.13-18.186, 18.4-21.5, 11	

Table 12. Measurements (\bar{L} , $\sigma_{\bar{L}}$, δL) of microtubules II-3 of microtubules.

	\bar{L}	$\sigma_{\bar{L}}$	δL	\bar{L}	$\sigma_{\bar{L}}$	δL
Overall length	80.894, 208, 21.3-36, 2.12	108, 1943, 209, 16.3-176, 8.3	11, 940, 105, 16.3-193, 8.3	74, 760, 814, 71, 1-81, 3.7		
Greatest transverse diameter at position and	74.334-8, 207, 14.9-18, 3.12	78, 1240, 204, 13, 1-21, 2.3	17, 3048, 113, 15.3-19, 7.5	71, 1140, 413, 70, 4-19, 6.7		
Greatest denudated diameter of proximal end	88.894-8, 413, 21.6-36, 2.11	27, 1040, 291, 16, 1-24, 2.3	13, 2048, 408, 13, 1-20, 8.3	74, 1040, 304, 71, 3-33, 5.7		
Transverse diameter at middle of shaft	72.304-8, 303, 19.3-17, 3.12	19, 1040, 209, 11, 1-19, 3.3	11, 3048, 318, 10, 1-12, 3.3	70, 1040, 318, 70, 4-11, 4.7		
Greatest diameter at middle of shaft	71.894-8, 208, 6, 5-12, 3.3	11, 1040, 403, 9, 1-10, 3.3	11, 3048, 103, 10, 3-11, 3.3	6, 1040, 304, 6, 3-10, 3.7		
Greatest transverse diameter at distal end of shaft	76.304-8, 413, 16, 3-36, 2.12	19, 1040, 204, 13, 1-21, 2.3	13, 3048, 103, 13, 3-13, 3.3	77, 1040, 312, 76, 4-19, 5.7		

The ventral base of this articular surface is broad, forming a strong attachment site for the interosseous muscle. On the lateral surface the dorsal facet for articulation with metacarpal II is not as elongate as in *h113*. There is no ventral facet distinct from the surface which articulates with the sesamoid. Contact with metacarpal II is weak at this point. On the external surface a facet for articulation with the sesamoid is present in three specimens. The facet for articulation with metacarpal IV tends to be broader and more convex than in *h113*. The dorsal side of the distal condyle is much flatter than in *h113*.

Metacarpal II of *glacialis* (table IX) is similar to that of *h113 sens*, but is somewhat straighter. The dorsal facet articulating with metacarpal II is joined to the sesamoid facet by a shorter neck on the proximal surface. The facet articulating with metacarpal IV is continuous and does not vary much in width.

Metacarpal IX. In *harpagornis* (table VI) the proximal articular surface in proximal view does not appear to be as expanded laterally as in *h113*. This is because the ventral facet for articulation with metacarpal III is at a greater angle to the proximal surface, as much as 90° in some specimens. The dorsal facet for metacarpal III has a much broader connection with the proximal sesamoid facet than in *h113*. The facet articulating with metacarpal V is convex in section, not flat as in *h113*. There is no proximal interosseous muscle scar on the ventral surface.

The proximal articular surface of metacarpal II of *Alcedinides* (table IX) differs from that of *h113* in several aspects. The dorsal

border for articulation with metacarpal III contacts the unctiform facet further ventrally and is more separate from it. The ventral facet for articulation with metacarpal III is not distinct from the unctiform facet.

Metacarpal II The proximal surface articulating with the unctiform in harpagornis (Table II) is narrower and extends further distally on its dorsal portion than in tyto. In the external part of the ventral border of this surface is a hook-like process for muscle attachment. In the lower surface the facet for articulation with metacarpal III is concave, not flat as in tyto. The dorsal shelf which gave support to this articulation is continuous with this facet and is not as prominent and distinct as that of tyto. The ventral portion of the facet does not bend dorsally. In the proximal part of the lower surface the tuberosity is large, sloping and concave. The shaft is triangular in cross-section. In the external palmar surface there is an elongate knob for muscle attachment. The distal end of is asymmetrical and has a rounded dorsal border as in tyto.

Metacarpal IV of harpagornis (Table II) tends to be more slender than that of tyto. The lower projection at the proximal end supporting articulation with metacarpal V is smaller and more dorsal in harpagornis. To the palmar side of this projection the notch that indicates the margin for the facet for metacarpal III is much shallower than it is in tyto or it may even be absent.

Intermetacarpal bones The pairs of intermetacarpals has many characteristic features distinguishing it from that of tyto.

In lateral view the wing of the filum, the ala, is rotated medially into the horizontal plane. Its external surface is well excavated for the notal gluteal muscle. There is no ventral iliac spine. The body of the filum is thick, but relatively narrow distally. In lateral view the body continues anteriorly to the crest of the filum. The body is separated from the ala by an abrupt transverse constriction. The iliopectineal eminence is a very prominent, anterior-posteriorly elongate knob. The ventral gluteal line continues toward the crest from the anterior end of the iliopectineal eminence, marking the sharp division between the dorsal and ventral surface of the filum. The whole ventral surface narrows and curves laterally anterior to the vertical surface. There are, therefore, relatively large areas for attachment of the filar muscle on the ventral surface and the deep gluteal muscle on the lateral surface. The greater ischiatic notch is short, markedly concave and sharply defines the posterior boundary of the ala. It terminates anteriorly at a prominent posterior dorsal iliac spine. The ischium is relatively short. The body of the ischium is rotated laterally to a greater degree than in *fulig*. The ischiocollis tubercle is prominent and extends further posteriorly than in *fulig*. The ischiocollis spine is moderately developed. The cranial branch of the pubis is turned to lateral aspect. The tubercle for the pectus minor is prominent.

The petiole of *Blattaria* has characters of both *Scutellon* and *fulig*. The ala of the filum is less convex than either of these two genera, but is otherwise similar to that of *fulig*. The greater ischiatic notch is very shallow and the posterior iliac spine is

poorly developed. The cranial branch of the paria is relatively short. The faciliotic spine is weakly developed.

Imag. The femur of farboursalis (Table 11) is not proportionately heavy for its size. The surfaces for muscle attachments, however, are much more prominent than those of falids. The shaft is bowed caudad anteriorly to an area greater extent than is seen in falids. From the level of the third trochanter the proximal portion of the femur is bent anteriorly, giving the femur a slightly S-shaped profile. The shaft is flattened posteriorly. The head of the femur is on a long neck and rises above the level of the greater trochanter. The valley between the head and the greater trochanter is relatively wider and deeper than in falids. The surface for muscle attachment of the greater trochanter occupies a greater area on the external surface, extending distally to the third trochanter. The greater trochanter does not extend laterally along the anteroposterior border where there is a large triangular surface for the pyiformis muscle in falids. Instead there is a slight crest running distally along the anterior surface from dorsal-external corner of the greater trochanter. The lesser trochanter is much larger and is situated relatively more distally than in falids. The distal fossa is not as deep as in falids. There is a small but elongate third trochanter. Initially, the posterior groove is shallower than that of falids. The two condyles are roughly equal in size and the intercondylar notch is narrow.

The femur of blatariasi (Table 12) is elongate and slender. The shaft is elongate and circular in cross-section, except proximally

Table T3. Honeycombs of the Pines.

	Nucleocapilla			Microdasy		
	N	T	L.A.	N	T	L.A.
Overall length from tip of greatest crocheter to distal vertex	1		(475)	1		(460)
Transverse diameter of proximal end, outer face of greatest crocheter to inner side of head	1	20.50±0.60	79.3-79.1	2.8	19.40±1.00	64.6-76.0
Greatest internode diameter at base	1	31.04±0.40	80.6-81.1	4.1	23.30±0.60	50.4-58.2
Transverse diameter of shaft at middle	2	26.50	78.2-78.1	3	24.00	56.1-62.6
Internode diameter of shaft at middle	2	21.20	79.4-79.2	3	21.00	56.6-58.6
Greatest width of distal extremity	4	64.00	82.5-84.6	3	61.00	53.5-64.1
Greatest subapical diameter of distal extremity	4	64.50	80.2-81.6	3	64.20	52.4-60.1
Greatest width of internode with	4	16.00	50.4-51.6	3	16.20	56.3-60.6
Greatest width of triangle surface of lower node	4	21.50	61.2-64.6	3	22.00	51.2-64.6

and distally where it is slightly flattened posteriorly. The neck is short and the head is below the level of the greater trochanter. The greater trochanter extends further anteriorly as its posterior side than it does in folia. On the external side it extends further distally, to a level below the lesser trochanter, from where it continues extended further as a slight crest. The second trochanter is a large knob that is situated relatively closer to the head than in folia. The distal fossa is larger and deeper. The distal condyle and the patellar groove are relatively narrower laterally than in folia. The patellar groove is deep and extends further proximally into the shaft. The external condyle is larger than the internal condyle and the two are separated by a wide heterocylindrical notch.

folia. The tibia of hachouryfolia (Table 14) is a reasonable short bone. The proximal surface does not extend as much beyond the shaft as in folia, especially laterally. The articular facets for the femur are relatively flat and roughly equal in size. The gap between the two spines, the angle between the two facets, is shallower and very narrow. The proximal tibial articular facet is large and is situated close to the proximal surface. In lateral view the tubercle for attachment of the ligamentum patellae is located relatively far distally. In this view the border makes a much more gentle descent to the proximal surface than in folia. The coronal crest is well marked and extends approximately halfway down the shaft. Proximally on the internal surface the area for the insertion for the tibialis anterior is poorly defined, without well defined dorsal and proximal borders. In ventral view the shaft broadens dorsally

Table 14. Measurements of the rivets.

	d	Ends of rivets			R	Rivets		
		T	δ	δ_0		T	δ	δ_0
Greatest length	11	106.32±.76	300-318	3.1	4	102.4	104-108	
Greatest transverse diameter of pinhead and	16	14.32±.70	55.5-58.7	4.4	5	16.31±.43	15.5-16.8	4.8
Transverse diameter of shaft at middle	16	18.05±.36	15.5-15.8	5.2	4	21.76	19.4-23.7	
Greatest transverse diameter of shaft and	16	15.12±.83	16.5-18.8	6.7	11	18.02±.11	18.0-17.1	6.1
Greatest subequatorial diameter of shaft and	16	22.45±.87	20.5-23.1	4.5	11	36.37±.44	28.3-34.0	7.1

and ventrally. The ventral surface below the head is deeply and broadly excavated. Finally, the two processes on the medial surface for the heads of the fibular stylopod longus and the third's posterior are well defined. The distal notch is the distal end. It is even shallower than that of *Leptochela*.

The tibia (table 14) of *Chirostylus* is an elongate, slender bone. The articulating surfaces with the femur are similar to those of *Lept.* The tubercle for attachment of the ligament posterior is less inclined distally. The tubercle shows ventrally resulting in less margination between it and the lateral condyle than there is in *Lept.* The ventral surface below the head is shallowly excavated and the posterior notch between the two condyles is broad and shallow. The nutrient foramen opens on the ventral surface as in *Lept.* The anterior notch is the distal end and is deeper than in *Lept.*

Adiantum. The coxal surface of the coxapophysis of *Leptochela* (table 15) is broad and extremely shallow. A well developed subcircular foramen is present in all specimens. The notch is short and wide. The articulating surface for the merostoma is rounded and does not project very far laterally. The articulating surface for the fibula occupies nearly all of the external surface. On the ventral surface the external facet for articulation with the ulnareum is much less concave than that of *Lept.* The third facet is broadly connected to the third facet for articulation with the ulnareum. This third facet is not delimited from the merostoma facet. These two ulnareum facets and the merostoma facet form a

Table 10. Measurements of targets

	Inches/ft			Mils/cm		
	N	I	St	N	I	St
CC-000420						
Instant length	10	20.205-20.3	20.2-20.3	0	40.005-40.6	40.0-40.2
Instant width	10	20.4-20.5	20.4-20.5	0	40.7-40.8	40.7
Instant thickness across web	10	17.005-17.1	16.9-17.0	0	34.0-34.1	34.1
Instant thickness of band	10	21.405-21.5	21.2-21.3	0	43.005-43.1	43.0
CC-000421						
Instant length	10	30.405-30.5	30.3-30.4	0	60.805-60.9	60.8-60.9
Instant width across rectangular flange and leg	10	20.205-20.3	20.1-20.2	0	40.4-40.5	40.4
Instant width across flange surface measured along rectangular flange and leg	10	19.6-19.7	19.5-19.6	0	39.2-39.3	39.2
CC-000422						
Instant length	10	20.205-20.3	20.1-20.2	0	40.4-40.5	40.4
Instant width across flange surface measured along rectangular flange and leg	10	19.6-19.7	19.5-19.6	0	39.2-39.3	39.2
CC-000423						
Instant length	10	20.205-20.3	20.1-20.2	0	40.4-40.5	40.4
Instant width across flange surface measured along rectangular flange and leg	10	19.6-19.7	19.5-19.6	0	39.2-39.3	39.2

continuous convex surface. Articulation between the astragalus and the calcaneus is very loose, with a good deal of rocking and some sliding possible between the articular surfaces of these two tarsals. The groove for the interosseous ligament is not constructed by the medial calcaneus facet and is relatively wide.

The trochlear surface of the astragalus of *Phocaena* (Table IX) is a little shallower than that of *Felis*. The astragalar foramen is variably developed. It is obsolete in about one-fourth of the specimens and is incomplete, but at least present distally, in the rest. The external articular surface is more vertical than in *Felis*. The neck is long. The articulating surface with the scaphoid is gently rounded and oval in outline. The long axis of the oval is at about 60° from a line drawn across the top of the third articular surface in distal view. On the ventral surface the external facet for articulation with the calcaneus is broader than that of *Felis*. The internal facet is anteroposteriorly elongate and is connected to the third facet by a short narrow band. The groove for the interosseous ligament is narrow and is constructed by the internal facet.

Calcaneus. The calcaneus of *Phocaenoides* (Table IX) is small with a short neck. The head is rounded and lacks a well defined groove for the heads of the plantaris muscle. The three astragalar facets are situated relatively close to the cuboid border. The external facet is an elongate band that is set at an angle as that of *Felis*. The two internal facets are very broadly separated, with almost no constriction to deflect the facets from the connection,

especially the anterior facet. The medially directed costovertebral facet is supported by a stout process on the external side, the costal process which serves as the origin for the external oblique muscle and quadratus lumborum muscle is relatively well developed.

The vertebrae of Hyomys (Table 16) is lyre-like in form and has a long neck with a grooved facet. The lower triangular facet is more circular in outline than that of Exocoetis, but is of course, the costovertebral facet is located even less internally than that of Exocoetis. It is circular in outline and is separated from the external facet by a narrow groove. The costovertebral facet is connected to the medial facet by a narrow band that runs parallel to the long axis of the vertebra. The costovertebral projects laterally from the body of the vertebra and is separated from it by a distinct medial groove.

Myxodonta. The vertebra of Myxodonta (Table 14) has a very concave posterior surface for articulation with the subcapitulum. This facet is more circular than that of Exocoetis. The dorsal and the anteroventral borders of this facet extend as far proximally as the intervertebral border. This facet does not extend as far ventrally as that of Exocoetis. On the distal surface the facets for the uncus, pterygoid and especially the antepterygoid are relatively larger than those of Exocoetis. All three uncus facets together occupy a greater proportion of the distal surface than they do in Exocoetis. The space for the intervertebral ligament is restricted by their

ventral expansion). The medial facet is very large and occupies most of the external surface.

In the mandible of *Blennius* (Table 11) the proximal surface is somewhat more concave than that of *Pagrus*. The subarticular border extends further proximally. In the distal surface the facet for articulariform is larger than that of *Pagrus* and is situated closer to the ventral border.

Labridae. In *Archamia* (Table 11) the proximal and distal articular surfaces are relatively quadrate. The articular surface for articular III is very small. The tubercle on the ventral surface is situated relatively far from the proximal end. In *Blennius* (Table 11) the proximal and distal surfaces are not as lateromedially elongate as in *Pagrus*. The tubercle on the ventral surface extends to the medial boundary. The tubercle is well developed and overhangs the groove for the previous longest muscle.

Sciaenidae II. In *Archamia* (Table 11) the proximal surface is relatively wider both dorsally and ventrally than it is in *Pagrus*. The surface for articulation with the mesoarticular occupies the dorsal 70% of the proximal surface and is shaped into a figure 8 that is wider dorsally and constricted ventrally. The ventral extension of the proximal surface is part of a large hook-like process for attachment of the interosseous muscle. On the lateral surface the ventral facet is divided into a proximally sloping distifacet for articulation with the articulariform and a distally sloping distifacet for articulation with articular III, and a single concave facet as in *Pagrus*. The distal condyle is more symmetrical

Table 8. Measurements (\bar{X} , $s\bar{X}$, $S.X$, W) of sections with 11.7 of *Peromyscus* sp.

	12	13C	28	3
Greatest length	25.144-405; 2.3-4.06 $s\bar{X}$, 3.3	33.35; 61.3-66.3, 3	44.33; 63.3-67.3, 3	57.213-223; 13.3-15.3, 3
Greatest transverse diameter of premaxilla	12.394-307; 3.3-7.3, 3.3	13.35; 27.3-30.3, 4	13.33; 18.3-19.3, 3	
Greatest diastematal diameter of premaxilla	20.354-405; 15.3-23.3, 3.3	22.25; 31.3-34.3, 4	20.37; 32.3-37.3, 3	27.213-223; 15.3-16.3, 3
Transverse diameter at middle of shaft	9.204-307; 5.3-10.3, 3.3	13.37; 27.3-32.3, 4	10.37; 15.3-18.3, 3	1.394-212; 3.3-10.3, 3
Diastematal diameter at middle of shaft	3.394-307; 2.3-10.3, 3.3	14.35; 3.3-11.3, 4	3.33; 3.3-10.3, 3	1.374-200; 7.3-10.3, 3
Greatest transverse diameter at distal end of shaft	14.354-307; 10.3-17.3, 3.3	12.35; 18.3-19.3, 4	13.33; 13.3-15.3, 3	14.213-223; 12.3-15.3, 3

and flattened dorsally than is in Felis. In Stenoplesion (Table 17) the surface for articulation with the antimeropform is more concave than in Felis and more differentiated, especially on the external side.

Metatarsal III. In Archaeopteryx (Table 18) the proximal surface for articulation with the metapleniform is more pycnos than in Felis, especially asymmetrally. This T-shaped facet is more symmetrical, with the ventral and palmar the dorsal are less internally. On the proximal part of the external surface the ventral facet for articulation with metatarsal IV is smaller and rounder than in Felis. The dorsal facet is less concave. In the internal surface the ventral facet for articulation with metatarsal II is poorly developed. The proportions of metatarsal III of Stenoplesion (Table 17) are similar to those of Felis, not Archaeopteryx. The facets for articulation with metatarsal II are smaller and the ventral facet is rounder.

Metatarsal IV. The proximal facet for articulation with the cuboid is more rectangular in Archaeopteryx (Table 18) than it is in Felis. The external margin is straighter and the ventral margin less convex. In the internal surface the ventral facet for articulation with metatarsal III is smaller and rounder than in Felis. On the external side the facets for articulation with metatarsal V are continuous. The shaft is relatively straight. The distal condyle is only slightly offset, about to the same degree as in Salicinctus, indicating that the toe was only bent slightly inward.

Metatarsal IV of Bufo (Table 17) is elongate and curved as in gills. The proximal articular surface is wide rectangular, with the external corner not extending as far forward and upward along the dorsal surface. Metatarsal IV of Sphecopterus is elongate, but is more massive than in gills or Chiroptera. The shaft is straighter and is dorsoventrally flattened distally. The distal condyle is only slightly beveled, about as much as in Scaphiopus.

Metatarsal II in Scaphiopus (Table 18) the proximal surface for articulation with the cuboid is large and elongate, extending to the ventral lateral corner. There is no wing-like proximal surface; however, there is a prominent lateral knob with a dorsal spine attachment at the base of the proximal tarsus and navis and the abductor digiti quinti. On the lateral surface there is no distinct ventral facet for articulation with metatarsal IV. The dorsal facet does not project medially from the shaft, as it does in gills. The shaft is triangular in cross-section in most specimens and has a well defined lineal keel on its ventro-external edge. The distal condyle is broader externally. Metatarsal V of Bufo (Table 17) is very similar to that of gills. The proximal wing-like process is not as well developed and the dorsal articular surface with metatarsal IV is smaller in Bufo.

Chalcids. There are numerous unassociated challenges from the literature but nearly all of the larger ones are folded in construction, but they are difficult to assign properly. The proximal challenges appear to be divisible into two categories. One has usual gills proportions. The other is wide proximally and tapers distally

Table 17. Parameters (L, p₀, p₀, n) of distributions II-4 of intercity.

	II	III	IV	V
Greatest length	127.100-1.000. 100.0-100.0.0	115.100-1.000. 100.0-100.0.0	117.000-1.000. 110.0-100.0.0	111.000-1.000. 110.0-100.0.0
Greatest transverse diameter of protrusion	16.000-1.000. 16.0-16.0.0	16.000-1.000. 16.0-16.0.0	16.000-1.000. 16.0-16.0.0	16.000-1.000. 16.0-16.0.0
Greatest diameter of diameter of protrusion	20.000-1.000. 20.0-20.0.0	20.000-1.000. 20.0-20.0.0	20.000-1.000. 20.0-20.0.0	20.000-1.000. 20.0-20.0.0
Transverse diameter at middle of shaft	11.000-1.000. 10.0-10.0.0	11.000-1.000. 10.0-10.0.0	11.000-1.000. 10.0-10.0.0	11.000-1.000. 10.0-10.0.0
Diameter of diameter at middle of shaft	11.000-1.000. 10.0-10.0.0	11.000-1.000. 10.0-10.0.0	11.000-1.000. 10.0-10.0.0	11.000-1.000. 10.0-10.0.0
Greatest transverse diameter at distal end of shaft	17.000-1.000. 16.0-16.0.0	17.000-1.000. 16.0-16.0.0	17.000-1.000. 16.0-16.0.0	17.000-1.000. 16.0-16.0.0

and is even as long as the longer Eclyp-like pharyngeals. The proximal articular surface is not as high dorsomedially and is more inclined proximally along the dorsal surface. The distal-most articulations of Barbagordalla articulate better with these pharyngeals. The convex-sided articulations of Stenoclydes articulate best with the Eclyp-like pharyngeals. The medial pharyngeals show a great deal of variation in the amount of affix to the distal articular surface, however, there is almost no such variation in the right medial pharyngeal in Eclyp. The medial pharyngeals that articulate best with the proximal pharyngeals associated with Barbagordalla show somewhat less affix than those associated with Stenoclydes. However, all of these carried fully retractile claws. All of the large distal pharyngeals are hooked to at least some extent.

Stenoclydes, Barbagordalla and Stenoclydes differ strikingly in their postcranial anatomy. Stenoclydes is typically taller in structure and proportions, and in many features resembles the Japanese Eclyp (1964). Barbagordalla is decidedly non-fallic in structure, and resembles more closely the American Eclyp (1964). Stensberg (1961) detailed a list of osteological characters which he used to distinguish the phantagrade condition. Stenoclydes, in contrast, possesses the diptygrade characters he detailed for modern cetis.

Characters that Stensberg (1961) considered diagnostic of a phantagrade stance that are also present in Barbagordalla include the following. The limb bones are short and heavy. This is particularly true for the front limb. The bones of the hind limb are relatively short, with well developed processes for muscle attachment,

but are relatively slender. Joints in pleustigrae animals tend to be "looser" with a greater radius of action. In Archaeopeltis this is especially marked in the joint between the radius and scapholunar, which has a very rounded proximal articular surface, the joints between the postilli and metapodials and between the metapodials themselves, and the joint between the tibia and the astragalus, in which the astragalar teeth are poorly developed. The humerus possesses prominent proximal, distal and lateral epicondylar ridges, with the proximal and distal crests extending to base of the humerus. The femur possesses a strong third trochanter and relatively small distal condyles. The ulnae is short and the subarticular facet is medially situated. The astragalus possesses a short neck. The metapodials are short and, when articulated, spread out to a fan.

Reyes (1986) criticized Stensberg's (1987) work on pleustigrae posture and stated that all stenevrids and felids have digitigrade posture at least for the forelimb. Although this may be true, classifying all these caninivores as simply digitigrade masks important differences in their postures. The Oligocene stenevrids, certain euchaenodontine felids such as Sarcobates, and Archaeopeltis should be classified semi-digitigrade. Thus, although their metapodials were not in full contact with the substrate during locomotion, they were not nearly as perpendicular to the ground as in the fully digitigrade felines. Implications of this posture will be discussed below.

The limb proportions of Sphaerophis are most similar to those of the neophthalmine fish Squalius. Sayon (1976) computed limb-segment ratios for 12 sizes of Squali and Squali spp. The humerus-radius index (radius/humerus $\times 100$) ranged from 82.8 for Squalius to 104.2 for Squalius squalius, the smallest. In Sphaerophis laiet, the humerus-radius index based on the single complete humerus and the average radius length is 71.2. Extreme values using the largest and smallest radius are 71.7 and 70.6. A value of 71.7 was computed for a radius and humerus, possibly from the same individual, of Sphaerophis from Long Island Sound, New York in the USNM collection; these values are all markedly lower than those reported by Sayon (1976), but are closest to those reported for Squalius.

The femur-radius index (radius/femur $\times 100$) ranged from 85.7 for Squalius to 106 for Squali spp., the snow leopard, and S. squalius. The value for Sphaerophis laiet, based on the estimated length of the single nearly complete femur and the average radius length, is 76.8. Extreme values are 76.4 and 75.3. The average index for two femora and two thirds of S. fricki in the USNM collection from the Jack Sayon Quarry in Kansas is 84.6. Again, these values are smaller than those reported for Squalius.

The intersegmental index (anterior limb length/posterior limb length $\times 100$; anterior limb length = length of humerus + radius + third metacarpal; posterior limb length = length of femur + tibia + third metatarsal) ranged from 78.0 for Squalius and 81.0 for Squali spp., the suna, to 87.4 for Squalius. The average value calculated for Sphaerophis laiet is 81.8, close to that of Squalius.

Sorex [10M] correlated the heterophilous and homophilous features in forest rodents with inhabiting highly structured habitat, such as dense forest, high rodents, with inhabiting open terrain. He correlated elongated hind limbs, such as are present in Eutamias, with jumping ability. According to Sorex's criteria, Peromyscus was an inhabitant of dense forest. A fully digitigrade posture is best adapted for running down and capturing prey in open country. The semi-digitigrade Peromyscus probably stalked and ambushed its prey in the dense forest, perhaps along the stream border of the channel that formed the low flow bed. Sorex also used the relationship between the cross-sectional area of the humeri and its length as an indication of the size of prey that a rat could capture. The cross-sectional area was computed by multiplying the width and thickness of the shaft two-thirds of the way down the shaft. The cross-sectional area of the complete Peromyscus humeri is 661 cm^2 . This value falls well above Sorex's calculated regression line, indicating that Peromyscus probably took prey substantially heavier than its own body weight, such as Peromyscus or Peromyscus.

Suborder Eulipotyria

Family Procyonidae

Procyonidae: Procyonidae are among the most diverse of all mammal orders. Recent members of this family, which includes Procyon, the raccoon, Canis, the wolf-dog, and Canis lupus, the ring-tail

or sacrocaudate, are relatively common and wide ranging. Hoser (1944) attributes their poor representation in the fossil record to their usual arboreal habits. All of the living genera climb well, although *Chama* and *Procyon* spend most of their time on the ground. It is likely that most of the fossil Procyonidae were also to some extent arboreal. Procyonids are also typically forest dwelling, a habitat rarely sampled in the fossil record. Much of their evolution may have taken place in Middle America, where the majority of North American procyonids are found today. Although this region has a very poor fossil record, it is known to have maintained a lush subtropical vegetation throughout the Tertiary (Graham, 1972, 1973).

With the exception of *Basileuterus*, none of the living genera has had a pre-Miocene (Pliocene) fossil record. Taxa that were thought to be ancestral to the higher Procyoninae, such as *Chama* or *Leontideus* from the early Miocene of North America (Hobbs, 1930) have been shown to be Canidae, and are therefore unrelated to procyonids ancestry (Gahr, 1943; Rough, 1944). The only previously known Miocene North American non-human primate procyonid, *Elaphocyon* (Gillson, 1940) from the Huerfania of Texas, was described as having dubious relationships with the living procyonids. The material described in this paper helps to fill the late Tertiary void in the history of the New World eumetatherian procyonids. *Elaphocyon* is shown to be the primitive sister taxon to these higher procyonids. This material also helps to clarify the relationships of *Procyon* and *Basar* to each other and to other Procyoninae. It also clarifies the origins of the earliest South American Procyonidae of the *Cynictidae*

grisea (Kriegerovich and Reig, 1954, Kriegerovich and Olsufev, 1955) and shows them to be related to the new North American genus *Antennosia*.

Genus *Strophosoma* Wilson

Strophosoma *Strophosoma* *Strophosoma* Wilson, 1955

Genus description: Larva curved and slender. Short distance between P^1 , P^2 and P^3 . P^4 with paracoxae-metacoxae blade, postero-internal cingulae, large protocoxae and small hypocoxae. P^5 and P^6 with well developed subcoxal and internal cingulae. Prescutilla elongate.

Strophosoma *Strophosoma*, n. sp.

Fig. 130, 1, Table 15

Material: 1 AM 45114, left prescutilla and maxilla with P^{1-3} , C^1 , P^{1-3} , P^{3-5} . Same data type only.

Loc. locality: Barker Creek Quarry, Lower Cambrian Formation, Green County, Nebraska.

Age: Middle Cambrian.

Figure: 1. Larva, lateral.

Remarks: P^4 with incipient parastyle and small hypocoxae. P^5 with anteriorly placed protocoxae, joined to large metacoxae.

Description: The dorsal margin of the infra-orbital foramen is broken, but it appears to be large and oval with a vertical diameter of about 4-5 mm. The prescutilla is elongate, continuing

Figure 12: Elaphoglossum lucidum and Argyranthemum flavidum.
Elaphoglossum lucidum, F. BR 45718, left: perianth and
 corolla with 1^{-1-3} , 2 , 3^{1-4} , (A) nodal view, stereo-
 pair; (B) lateral view (both $\times 1$). Argyranthemum
flavidum, nodal view, stereopairs (all $\times 1.5$),
 (C) of 24342, left P_1^L ; (D) of 24343, left W^L ; (E)
 of 24348, right P_4 ; (F) of 24354, left W_1 .



A



B



C



D



E



F



G



H



I



J



K

Table 16. Measurements taken on *Scaphium laticornis*.

	length	width
ℓ^1	4.3	3.5
r^1	3.3	2.4
r^2	5.8	3.2
r^3	6.3	3.9
r^4	6.7	3.6
g^1	6.6	5.0
g^2	6.3	3.8
$r^1 + g^1$	12.4	
$r^2 + g^2$	10.4	

posteriorly to at least the P^1-P^2 distance. The incisors increase in size from I^1 to I^2 . The canine is oval in cross-section.

P^1 . Single-rooted, with a single cusp directed anteriorly.

P^2 . Wide cusp with long posterior heel, weak postero-internal cingulum; minute posterior accessory cusp.

P^3 . Nearly symmetrical wide cusp, with minute posterior accessory cusp. Tooth expanded postero-internally.

P^4 . Long posteriorly directed paracone separated from blade-like ectacone by a narrow notch. Prominent cervical protocone at antero-internal border of tooth. Anterior cingulum slightly inflated externally, forming an incipient annulete. Posterior cingulum with small hypocone.

P^5 . Subequal paracone and ectacone connected by a crest. Protocone anterior to the midline of the tooth. Mesocostals separated from paracone by a narrow shallow cleft. Preprotocristae and postprotocristae pass anterior and posterior to the paracone and ectacone, respectively, joining external cingulum. Paracone joined to ectacostals by short crests. Hypocone formed from a swelling of the internal cingulum at postero-internal corner of tooth. The anterior cingulum is slightly swollen at its labial termination.

P^6 . Smaller than P^5 . Subtriangular occlusal outline. Paracone and ectacone subequal. Narrow notch separates ectacostals from large protocone. Preprotocristae and postprotocristae and ectacostals to ectacostals identical as in P^5 . External cingulum moderately developed, internal cingulum well developed, especially posteriorly.

Comments. Diagnosis. Index is larger than 1. Coordinate is

The P^1 has a long well developed parastyle, hyomeres, and infernal stipules. The telome is larger and form a longer parastyle-entostome blade. The P^2 has a more anteriorly placed phlebotome with a more prominent entostoma on its posterio-anterial flank. The hyomeres is a little smaller than in [*Arctostictus*].

Arctostictus, n. gen

Arctostictus varius Arctostictus floridanus, new species.

Included species: Arctostictus floridanus, new species, Arctostictus niger, new species, Arctostictus grayii, new species, Arctostictus nuchalis, new species, Arctostictus franks, new species.

Comments: Mr. Arctus, a bear, also northern, also Arctus, the south-west, is commonly with other genera and of this family.

Diagnosis: P^1 with parastyle present, entostome very reduced to absent, and protostome placed relatively posteriorly, P_2 with antostome separate from entostoma and reduced parastyle, mandible elongate and tapering anteriorly.

Remarks: Measurements of the species of Arctostictus are given in Table 78. Important dental characters are summarized in Table 39.

Table 20. Selected characters of the species *Arctostaphylos*. A dash (-) indicates that a character could not be determined.

	λ_1 reflexa	λ_2 praefolia	λ_3 floribunda	λ_4 purpurata	λ_5 dracoid
λ^0 rubraeae praeaeae lythraeae	absent various very small	very light purplish white	absent various white	absent various white	- - -
λ^1 caeruleae caeruleae caeruleae caeruleae caeruleae	absent present absent absent absent	absent present absent absent absent	present present present present present	- - - - -	very small present present present present
λ_6 foliolae	-	various	white	white	-
λ_7 caeruleae triglobae	reduced large	reduced absent	reduced absent	absent absent	- -
λ_8 albae albae	α_1 -	α_1 present	α_1 present	α_1 present	- β_1 absent

Polianthus flavifrons, n. sp.

Fig. 10C-F, tables 1b, 3b

Holotype. W 3482, left P^1 .*Type locality*. Lava Bone Bed, Alachua Formation, Alachua County, Florida.*Age*. Latest Cretaceous.*Diagnosis*. Holotype plus W nos. 3483, left P^1 , 3484, right P^1 , 3485, left R_1 ; 3486, right R_1 , 3487, right R_2 , 3488, right R_3 .*Etymology*. Named for Florida.*Diagnosis*. P^1 with hypocoxa and large protocoxa and with antecoxa absent; R^1 with complete cingula and paracoxula; P_2 with large telonot; R_2 smaller than R_1 .*Description*. P^1 . Subtriangular aciculi anterior; protocoxa larger than paracoxa, parastyle prominent, hypocoxa connected to protocoxa; lateral cingulum weak. R^1 . Much larger than P^1 or P^2 , anterior, posterior, internal and external cingula present, hypocoxa reduced to a cingular crest posterior to the large protocoxa, paracoxula and antecoxula small; paracoxula slightly anterior to paracoxa, paracoxa larger than antecoxa; subquadrate occlusal outline. P^2 . Longer laterally than lingually, internal cingulum well developed, antecoxa smaller than subequal paracoxa and protibiae, hypocoxa absent; paracoxula and possible antecoxula on preapical cingula and postpreapical cingula, lateral cingulum absent.

P_4 . Prebasal lobe, occupying approximately anterior half of tooth; hollows posterior accessory cusp on labial border of tooth, well developed posterior cingular cusp labial to hollow of tooth, slight crest runs along relation of main and posterior accessory cusps to posterior cingular cusp; labial basin formed by a (slight) and posterior ridge connecting main and posterior cingular cusps.

R_1 . Paracostal and entocostal separated by a narrow notch; paracostal smaller than protoconal or subequally labial longer and slightly lower than trisqual, separated widely separate from protoconal, sublingual short; entocostal opposite hypoconal and connected to it by a low ridge, descending anterior and posterior labial basins, small entocostal at bottom of valley between entocostal and anticonal; big cusps are present on the postlingual.

R_2 . Metacostal is the largest cusp, antecostal and protoconal connected by an anterior cingular; antecostal slightly posterior to hypoconal, hypoconal broken, but was probably similar than the other cusps.

PREMAXILLAR DENTITION, A. sp.

Fig. 14A,C,D,F, Tables 19,20

holotype. P_1 AM 105249, right mandible with P_2 - P_3 , premaxilla and maxilla fragment with left and right L^{1-3} , P^1 , and rc^1 , and detached left and right P^2 - m^2 . Given from holotype only.

Type locality. Spillhoff local fauna, lowermost Valanginian Formation, Irga Paha County, Borneo.

Figure 14: *Archaeopteryx gracilis* and *Archaeopteryx cf. gracilis*. *Archaeopteryx gracilis*, ROM 100198, (A) right dentary with P_{100} , P_{11-12} , occlusal view, stereopair (x 1); (C) right r^A , occlusal view, stereopair (x 1.5); (D) right r^B , occlusal view, stereopair (x 1.5); (F) same as (A), internal view (x 1). *Archaeopteryx cf. gracilis*, (E) ROM 100198, right dentary with P_{10} , occlusal view, stereopair (x 1); (G) ROM 100198, right r^B , occlusal view, stereopair (x 1.5); (H) same as (E), internal view (x 1).



A



B



C



D



E



F



G



H



I



J



K



L

Egg. Late hatching.

Development. L. gracilis, slender

Imagines. I^1 with vestigial setae, I^2 with setaceous and parasetae absent, and small apophysis posterior to pretarsus. H_2 much smaller than H_3 .

Description. The pronotum and scutella frequent latrodes that the face was long and narrow. The labellum increases in size from I^2 to I^3 . I^1 and I^2 are slightly apodetic.

C^1 . Slender, elongate, curved, oval to cross-section

I^1 . Single-rooted, single anteriorly directed cusp, separated from C^1 by an θ in thickness.

I^2 . Single-rooted, accessory cusps absent, broader posteriorly, with posterior-lateral and anterior cusps.

I^3 . Large central cusp with small anterior, posterior and internal cingular cusps, posterior-lateral cingular branches anteriorly at internal cingular cusp just posterior to the middle of the main cusp.

P^1 . Three-rooted, subtriangular apical outline, apophysis lateral cusp, pretarsus not as tall, but more bulbous, base of pretarsus and parasetae contact, pretarsus slightly anterior to parasetae, parastyle connected to pretarsus by anterior cingular with minute cingular cusp at base of parastyle, setaceous and apophysis small.

P^2 . Subquadrata apical outline, pretarsus the largest cusp, prepretostyle and postpretostyle less anteriorly and posteriorly to the parasetae and slightly smaller setaceous, respectively.

A short ridge connects the paracone with the preprotostostyle and the entopogon with the entostomatid. The hypostome contacts the entostomatid, it is related to a posterolateral expansion of the internal cingulum. The internal cingulum is also slightly swollen at its anterolateral termination. Because of brevity, the extent of the external cingulum cannot be determined.

P_1^2 . Subtriangular occlusal outline, paracone larger than entocone. Posterior portion of the internal cingulum is continuous with the postprotostocingulum.

The mandible is broken anterior to the P_2 . The alveolus for the canine indicates that it was probably a slender tooth, separated by a wide distance (including a P_3) from the P_2 .

P_2 . Small, rootless, uncusped, with a long posterior lobe.

P_3 . Separated from such smaller P_2 by a 4 mm distance, slightly anterior to P_4 , postero-lateral cingulum with posterior cingular cusp.

P_4 . Large posterior accessory cusp as posterolateral flank of main cusp. Posterolateral cingulum well developed with a posterior cingular cusp, anterior cingulum weak.

P_5 . Triangular lower than wide cusp on P_4 , paracone reduced, separated from entocone by narrow notch, lateral cingula, wider than lingual, hypostyle larger than entostyle, labial closed frequently by an entostomatid, hypostyled narrow.

P_6 . Smaller than P_5 , entocone larger than paracone, elongate oval with hypostyle, hypostyled and entostyle.

The mandible is elongate, tapering anteriorly. Two small

Foramina are present, one beneath the P_{2-3} distance, the other anterior to P_3 .

Description. Acinacera gracilis is smaller than A. floridana. It has a vestige of the acetabulum on the P^1 , lacks a pericardium on P^2 , does not have telson on P_4 as well developed and the telson on the P_5 is not as complex as in A. floridana.

Acinacera cf. gracilis

Fig. 145, L, A, Table VI

Referred material. F.M. 43264, right P^1 , F.M. 43265, right rema with P_1 .

Distribution. Trinity River cut 1, upper Fleming formation, San Jacinto County, Texas.

Age. Early Permian.

Description and comparisons. P^1 . Similar to A. gracilis, but notched within relatively shorter anteroposteriorly. External cirrus present.

Headfile tapers anteriorly, with slight deepening and bulging anterior to P_2 . P_1 is single-rooted and very small, separated from P_2 by a 1 mm distance. P_2 is double-rooted and separated from P_3 by a 1-2 mm distance. P_4 is worn, but is apparently similar in size and morphology to A. gracilis, except for a slightly more open trapezoid.

Archaeoscutum murina, n. sp.

Figs. 75, 76A-B; Tables 73, 20

Holotype. F-48 4814, left mandible with P_2 , R_1 .*Type locality*. Observation Quarry (Bosche Formation exposures)

Sweet County, Nebraska.

Age. Early Tertiary.*Diagnosis*. *S. sinuata*, modified.*Epistoma*. Holotype plus F-48 nos. 10244, left P^A , 48244, left P^I , 15334, left R_1 .*Epistoma*. Smaller than *Archaeoscutum gracilis*, P_2 not as reduced, R_1 with trigonal lobe compressed; P^I noticeably wider than P^A , articulation absent; P^A with articulation absent, protuberance anterior to and separated from paracone.*Paracrista*. P^A . Protuberance shorter than paracone, but subequal in width, separated from paracone by a narrow valley, articulation absent, small hypodent on posterior cingulum contacts protuberance; parastyle connected to small anterior alveolar cusp. P^I . Protuberance with crenulobaculosis and pseudolamellae joining anteriorly and posteriorly to the paracone and articulation, respectively. These two subventral cusps are connected to the articulation by short crests. The paracone and articulation were apparently connected by a crest. The internal and external cingula are well developed. The hypodent is a posterio-internal expansion of the internal cingulum. The internal cingulum is expanded at its antero-internal termination. R_1 . Uniserial, with a nearly vertical anterior edge and an elongate posterior lobe.

Figure 15. *Archaeopteryx lithuanicus*. F AM 46115, left dentary with P_2 , P_3 , occlusal and external views [x 1].



Figure 16: Archimedes mirror, Archimedes up—8, and Archimedes up—9
Archimedes mirror: (A) P+BB 45°/0, left assembly with
 P_2 , P_1 , occluded view, stereopair (a 1), (B) P+BB
 100°/0, left P^b , occluded view, stereopair (a 1),
 (C) P+BB 45°/0, left P^b , occluded view, stereopair (a2),
 (E) same as (A), lateral view (a 1). Archimedes up—8:
 P+BB 100°/0, (d) left auxiliary viewpoint with P^b , occluded
 view, stereopair (a 1-3), Archimedes up—9: P+BB 45°/0,
 (F) left P^b , occluded view, stereopair (a 1-3).



R_2 . Reduced paracostid separated from ariscostid by a narrow suture. Talonid longer and slightly wider than trigonid, subcostid smaller than hypocostid, larger than subcostalid. In P₁ at 2500, the cups are set as hollow as in the holotype, but are otherwise similar.

The mandible is relatively slender and is constructed virtually entirely to the P₂.

COMPARISON. *Archimedes* differs in the smallest species of *Archimedes*. It differs from *A. gracilis* in having R_1 with paracostid set as reduced, trigonid not as closed, and talonid not as elongate, P₂ not as reduced, h¹ set subquadrate, and hypocostid not as reduced and even uniform, and P² with protocostid more separate from paracostid, and ariscostid absent.

The h¹ of *A. gladius* is similar in morphology to that of *Cheloniceras pectinidens*, but the P² is characteristic of *Archimedes*.

Archimedes sp. A

Fig. 10f, Table 10

REFERRED MATERIAL. P 201208, left auxiliary fragment with P²-h¹.

LOCALITIES. Silver Place, Pelindaba Formation, Brown County, Nebraska.

Age. Late Santonian

Description and comparison. The two teeth in this fragment are worn and it is impossible to make a specific assignment. The P^1 has a subtriangular occlusal outline, a large paracost, and a parasyle. There is no evidence of a retucost. The P^2 is very heavily worn and broken. There is an external cingulum between the paracost and retucost. The teeth are larger than those of A_1 speciosa. They are slightly smaller than those of A_1 flaviluna, but the P^1 appears to be more symmetrical and the P^2 more triangular in the late Barabooian specimens.

Acromegium parvulus, n. sp.

(Fig. 12; Tables 34, 35)

Holotype. AMB 2422, right mandibular fragment with P_2-M_2 .

Type locality. Top channel in Pittsboro Gneiss, Johnson Harbor, Snake Creek Formation, Sioux County, Nebraska.

Age. Late Neoproterozoic.

Referred material. UF 2438, left mandibular fragment with P_1-M_1 ; UF 2439, left mandibular fragment with P_1-M_1 . Both from upper Snake Valley Formation, Polk County, Florida.

Diagnosis. Gr. large unspecialized, Gr. small are thin walls.

Comments. M_1 with paracost absent and cingula reduced, P_2 larger than M_2 and with cingula posterior half.

Description. The teeth are relatively low crowned and wear to form a flattened occlusal surface. The crown of the holotype, AMB 2422, is somewhat more convex than that of the Snake Valley

Figure 17 *Archosauia* outgroups: (A) *Arch. stict.*, right snout with P_{2-4} , R_{2-3} , occlusal view, stereopair (a 1); (B) *UF 24193*, left snout with P_1 , P_{1-2} , occlusal view, stereopair (a 1); (C) *stict.* as $(A)_1$, external view (a 2).



specimens, but the pattern of the major cusps is otherwise similar.)

P_2 . Bicuspidate, compressed, with short posterior lobe, slightly expanded labially, taller than P_1 .

P_3 . Bulbous, wider posteriorly, with large lobe occupying posterolateral quadrant of tooth, deep cusp with anterior cingulum and accessory cusp on posterolateral flank; posterior cingulum cusp slightly smaller than the posterior accessory cusp.

R_1 . Quadrate occlusal surface, small, especially of the anterior of the holotype, slightly complicated, labial much longer than trigonally protoconid and taller anticonid cuspids and subconid, connected anteriorly and by an anterior cingulum; low ectoconid between protoconid and hypoconid, anticonid between metaconid and paraconid; subconid and hypoconid separate, connected anteriorly in holotype, dividing labial in half, hypoconid on posterolateral corner of tooth.

R_2 . Larger than R_1 , well developed posterior lobe, protoconid opposite larger anticonid and connected by a straight anterior cingulum; anticonid, hypoconid and hypoconid smaller than anticonid, hypoconid adjacent to hypoconid at posterolateral angle of tooth, labial elongation between protoconid and hypoconid.

The mandible is thin ventrally, with a flat ventral surface beneath P_2 - P_3 . The ramus is massive below R_2 , with a well developed shelf for attachment of the anterior portion of the masseter. The masseteric fossa appears to be very deep.

Comments. *Archimedes* *variegatus* differs from other species of *Archimedes* in the loss of the ponsomed on the H_1 , in having H_2 larger than H_1 , its larger size, and its more lamellar dentition.

Archimedes fricki, n. sp.

Figs. 10, 11, Tables 18, 25

holotype. F.A.M. 50551, left ramus with H_2 .

Type locality. Highway 500, Canyon, Oklahoma.

Age. Late Mesozoic.

Diagnosis. Based on honor of Charles Frick.

Remarks. H_2 equal in size to H_1 and lacking alveolate posterior half, no diastema between H_2 and H_3 .

Epitype. Holotype plus F.A.M. nos. 50552, right H^1 , 50553, back of skull.

Description. H^1 with subquadrate postoral dentition, internal and posterior cingula well developed, anterior cingulus weak, external cingulus absent, small mesostyle present in narrow valley between molars and larger ponsomed, hypostoma a swelling of postorbital posterior to ponsomed, well developed ponsomed and antecostula connected to postcostula forming a V, prepostcostocuticularia extend anterior to ponsomed.

The holotype F.A.M. 50551 is a left mandible broken at the canine alveolus and with most of the ascending ramus broken.

The broken alveolus for the canine indicates that it was a relatively

Figure 16. *Arctomys frontalis*. (A) F.AN 58953, left mandible with H_{90} , occlusal view, stereopair (a 1). (B) same as (A), external view (a 1). (C) F.AN 58954, back of skull, dorsal view (a .87). (D) F.AN 49485, right H^b , occlusal view, stereopair (a 1 51). (E) same as (C), left lateral view (a .87). (F) same as (C), left zilla region, ventral view (a 1).

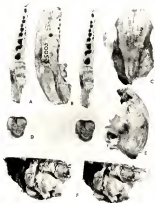
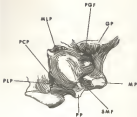


Figure 2b. Left auditory region of *Agostomus fricki*. Full view.
 Abbreviation: GP, glandular process, LP, median
 lacrimal foramen, MP, mastoid process, POF, posterior
 orbital foramen, POF, postglenoid foramen, PLF, post-
 erior lacrimal foramen, PP, paracryptal process,
 SF, styluslike foramen. See Figure 1b.



slender tooth. P_1 single-rooted, separated from P_2 by a short distance.

P_2 . Retained opposite mesial protocentrid, protocentrid, hypo-centrid and entocentrid subequal; hypocentrid on posterior margin of tooth between hypocentrid and entocentrid, margin of tooth indented between protocentrid and hypocentrid and between metacentrid and entocentrid.

The braincase is slightly compressed anteroposteriorly. It is broken anterior to the frontals and ventrally. Much of the occipital region is missing. The left ear region is well preserved, the right is detached from the skull and is badly broken. The braincase is markedly inflated. The paraseptal crests are well developed and extend from the posterior process to the supra-occipital, where they converge. The tentorial crest is extremely well developed and forms a concave ridge along the posterior angle of the parietal. The squamosal-parietal suture is raised. This does not appear to be a result of crushing, but is apparently for greater temporal muscle attachment. The frontal sinuses are greatly expanded beneath the anterior portion of the paraseptal crests.

In general the anterior braincase of *Hyliotes trichi* resembles that of *Desmanthus* lemn, especially *helianthi*, and of *Hylo-*. In *H. trichi* the frontal sinuses are more expanded and the paraseptal crests more widely separated than in *helianthi*. They both have the inflated squamosal-parietal suture. However, the posterior part of the squamosal (for attachment of m^1 temporalis pars profundus) is not expanded as far posteriorly as in *helianthi*.

or teles, although it is better developed than in other living Procyonidae.

The glenoid process is much longer than in other procyonines. The bulla does not extend below the glenoid fossa. The preopercular process is moderately well developed. The articular process is large and is not tapered or curved. The paracipital process is relatively large and in contact with the mastoid process and the bulla. A shallow groove, possibly for the stylhyoid muscle, extends anteriorly from the paracipital process, along the ventral surface of the bulla medial to the zygomaticotemporal suture, to about the level of the posterior zygotic foramen.

The auditory bulla is not adjoined to the skull, as is typical for the Procyonidae. The ectotympanic is highly inflated. The ectotympanic is only slightly elongated to form an auditory tube. However, a cartilaginous extension may have been present between the ventral and glenoid processes. The external auditory meatus is formed dorsally by the squamous and ventrally and laterally by the ectotympanic. The opening is circular in outline and is directed laterally.

The posterior zygotic foramen is in the medial wall of the bulla, approximately midway between the anterior and posterior margins of the bulla. The foramen is anterior and ventral to the posterior lacrimal foramen. The foramen canal lies entirely within the ectotympanic. The stylomastoid foramen is bounded anteriorly by the bulla, medially by the paracipital process, and laterally

by the mesothel process. The postglomerol fissure is at the medial edge of the glomerol process. Its posterior border is formed by the ectolymphatic.

The internal structure of the right bulb is difficult to determine because of damage. There is a suprenal space. An ectolymphatic recess and a fossa for the lesser tympanic are present, but their extent cannot be determined. The walls of the bulb form a complex of folds and creases, apparently at least partially dividing the anterior half of the bulb into dorsal and ventral regions as in *Scutigera* and perhaps *Cymatocera* (Pough, 1945).

A crack in the preantennal suture extends from the frontocranial suture. There is a beaklike tip above the frontocranial suture and median at the lateral border of the preantennation. The internal surface of the petiole resembles that of *Scutigera*. The lateral auditory vesicle is divided into two. The anteroposterior chamber is slightly larger than the posteromedial one. Each chamber contains two subequal-sized tympana: the large is the dorsal chamber for the facial nerve, the ventral for the auditory nerve. The appendicular fossa is larger than the lateral auditory vesicle. It is as deep as in *Scutigera* or apparently *Phalangium* (Hirst, 1960), but does not have as well a defined external lip.

Cymatocera. *Scutigera fricki* is differentiated from *S. garibai* on characters of the R_{4+5} . In *S. fricki* the anterior cymbula is much weaker, the heel is not developed, and there is morphological of the Tibial border between the retrolateral and antioral. In addition, the space in *S. fricki* is smaller than

that of *A. granulata*, especially that of the holotype from Snake Creek, and the H_2 does not appear to be as enlarged relative to H_1 .

Archaeosau. sp. B

Fig. 14F, Table 1B

Referred material. F AM 14916, left H^1 .

Distribution. Hollow Horn Bear Quarry, late middle formation, Todd County, South Dakota.

Age. Middle Cretaceous.

Description. Subquadrate occipital outline, crura caudally persons slightly larger than subacrom. or incipient personae may be demarcated by a cleft in the supra-external portion of the protacrom. strong anterior, posterior and internal cingula, weak external cingulae with small acanthyle, hypocrom. posterior to protacrom. posterior cingulae persistent median style.

Comparisons. The H^1 from Hollow Horn Bear Quarry differs from that of *A. flavigena* and *A. frigid* in its smaller size and in having personae and subacrom. were separate and in possessing a posterior cingular cusp. It differs from *A. granulata* in its larger size, posterior cingular cusp, well-marked personae, and possibly acanthyle.

Lithocrypta, n. sp.

Genotype species. Lithocrypta standard. See synopsis.

Included species. Type species only.

Diagnosis. Cr. lighter, gracile or robust, plus br. hyp., a dog, in conformity with outline of the family and several of the included genera.

Exopsis. P_2 approximately equal in size to P_3 , P_4 with trapezoid lower than wide quadr on P_4 , paracard separated from equi-sized metacard by a narrow valley, and trapezoid wider than triangular, P_5 shorter than P_6 , and angular process below level of mandibular teeth.

Lithocrypta standard, n. sp.

Figs. 20, 21A,B, Table 21

Material. F. 20 25210, right maxilla with P_2 - P_6 . Known from type only.

Type locality. Fort Clayton Quarry, Ash Hollow Formation, Green County, Minnesota.

Age. Early Clarendonian.

Diagnosis. Br. flexible, the apical teeth that rise from the alvea.

Remarks. Same as for genus.

Observations. P_1 apparently single-rooted, but relatively large.

Figure 25. Lichocroca phoenicea. LAR 16210, right view with R_2-R_3 , occlusal and lateral view (x 3, reversed).



Figure B5. *Uchisayacu phosphenes* and *Parasacantha kinshipica*.

Uchisayacu phosphenes, P-AM 20256, right manus with r_1^1 - r_{12}^1 . (A) occlusal view, stereopair (x 7); (B) occlusal view (x 7). *Parasacantha kinshipica*, HO of BMNH, left manus with r_1^2 , r_{12}^2 , occlusal view, stereopair (x 7); (C) of BMNH, left r_1^3 , occlusal view, stereopair (x 2); (D) of BMNH, right r_1^3 , occlusal view, stereopair (x 2); (E) of BMNH, right premaxilla and maxilla fragment, ventral view (x 7); (F) same as (E), external view (x 7).

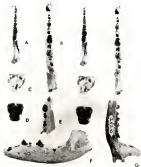


Table 21 Measurements taken on snoutless and lower sections of *Lichtheim, Larchmont, Mays, and Thomas*.

	snoutless	snoutless	snoutless	snoutless	snoutless
	1	2	3	4	5
C_1 length		(10.4)			4.8
					4.6
P_1 length	(7.8)	(5.2)			(5.8)
P_2 length	4.4	5.2		5.2	4.7
	3.6	3.6		3.1	"
P_3 length	4.4	(6.5)	6.8	5.8	5.3
	3.7		4.8	3.4	"
P_4 length	6.8	8.1	8.1	8.1	7.4
	5.5	5.8	6.7	4.9	"
P_5 length	8.5	(10.4)	(10.2)	(10.7)	8.2
	4.7				"
P_6 length	8.5	(8.4)	(8.4)	(10.4)	(8.7)
	3.6				
$P_1 + P_2$	22.5	46.1			41.8
$P_2 + P_3$	21.9	41.5		42.8	39.8
$P_3 + P_4$	19.9	29.3	36.8	36.5	25.8
depth below P_1	8.5	15.5	15.5	15.8	15.5
depth below P_2	8.5	14.4		14.7	

P_2 . Dent anterior cingulus, posterior cingulus with posterior angular tooth.

P_3 . Similar in size to P_2 , but with a stronger and broader posterior cingulus.

P_4 . Slender, but broadens posteriorly; posterior cingulus wider than anterior cingulus, until posterior accessory cusp on postero-external flange of same cusp.

P_5 . Protocord taller than subequal paracord and antecord, arranged roughly forms an equilateral triangle, but with protocord and antecord closer together, paracord and antecord separated by a deep valley; basial talonid wider and longer than trigonid, large hypocord at postero-external corner of talonid; hypocheilid narrow, antecord and antecordid separated by a narrow shallow notch.

P_6 . Antecord slightly larger than protocord; anterior cingulus continuous with narrow external cingulus between protocord and large hypocord; hypocordid at posterior apex of complete fan, hypocordid connected to hypocord by a ridge.

The genus is slender and elongate, but with only a short distance between P_2 and P_3 . The ascending ramus is inclined posteriorly. The mesosternum forms a shallow. Internally, a ridge between the P_2 and the articular condyle marks the ventral limit of the hemapophysis. The angular process is well developed and is situated below the level of the mandibular tooth row.

Chlorothraupis, n. gen.

Geographic variation.—Chlorothraupis hirundinacea.

Included species.—Type species only.

Etymology.—Gr. hiris, near, plus hiras, the earth-maid.

Diagnosis.— P_1^1 large and double-rooted; P^1 with setaceous smaller than parastyle, P^2 with external cingulum and reduced internal cingulum, R_2 slightly smaller than R_1 , with prebasal and antecubital subequal.

Illustrated description, n. sp.

Fig. 25a-f; labels 25, 25

Holotype.—OF 2455, left mandible with q_1 , P_{1-4} , R_{1-3} , R_4 broken.

Type locality.—Low Sand Bay, Alachua County, Florida.

Age.—Adult Chlorothraupis.

Etymology.—L. hiris, near, plus L. gras, root.

Diagnosis.—Same as for genus.

Specimens.—Holotype plus OF nos. 2457, identical right premaxilla and mandible fragments; 2459, left P^1 ; 2462, right P^1 ; 2463, left P^1 ; 2464, 2465, right P^1 ; 2466, right R_2 ; 2469, left mandible with P_2 , P_3 ; 2470-2473, redunculate mandible fragments.

Description.— P^1 .—Proximal anterior-internal to profound notched and connected to it by a ridge, hypoxone lower than

parastyle, notosone blade very reduced; internal cingulum between protocone and hypocone, circumscribed posterior cingulum terminates externally in a small antistyle on the notosone.

R_1^1 . Protocone and notosone subequal, rounded, mesostyle present. In one specimen, protocone with prominent cusp, preprotocrista passes anterior to the protocone; antiscutula posterior and slightly anterior to the protocone; parantescutal/crista passes posterior to antiscutula; hypocone small, internal cingulum confined posterior to protocone; internal axial slightly cristated in one specimen.

The lower carina is curved and segmented. P_1 is double-rooted. P_2 equal in length to P_3 , with cusp with short posterior heel and smooth anterior cingular cusp.

P_3 broader posteriorly than P_2 .

P_4 narrow anterior cingulum with anterior cingular cusp, broad but short postero-lateral cingulum with small posterior cingular cusp, posterior accessory cusp on postero-external flank of vein cusp.

R_1 . Rows from laboid only, laboid relatively short, trigoned and probably open.

R_2 . Slightly shorter than R_1 , multiple anterior cingula; large apocentral small antecardinal; flagell hypostomal.

The mandible is elongate, flake ventrally behind P_1 - R_1 , then curves upward posteriorly. The ascending mass rises very steeply behind the R_2 . No cingular processes are preserved, but they appear to be above the level of the mandibular tooth row. In the holotype the premolars are separated by diastemata. In other specimens they are more closely spaced.

Comparisons. The P^d of Larrea is similar to that of Procyon or Lynx. The rostrum is larger and the apiculus is smaller than in either of these two genera. The tooth is not as extended as far posteriorly as in Procyon. Lynx lacks an internal cuspation on the P^d . The P_4 of Procyon and Lynx are highly variable. The double-rooted P_3^1 's of Larrea are much larger than those of Lynx. Although the molars of Larrea are broken anterior to the cuspal process, the cuspal process apparently is above the level of the tooth row as in Procyon and Lynx.

cf. FIGURE 11

Fig. 11; Table 21

Referred material. F.M. 4861, Right mand with P_{3-4}

Locality. Oak Bayou Quarry, Texas.

Age. Early Miocene

Description. The teeth are worn and the jaw is distorted.

The mandible anterior to the P_3 and the ascending ramus are broken off. The P_3 is unisulcate with a posterior heel and is not compressed or elevated. The P_4 is narrow and elongate and is above the level of the mandibular tooth row. The mesostyle form is shallow. The alveoli for the M_1 are larger than for those of the M_2 .

Comments. The shape of the P_4 , especially the broad posterior heel, and the P_3 being smaller than the M_1 suggest that this specimen is a species of Paracynodon. The mandible is more massive than that of Paracynodon hesperus. The transition from

the horizontal ventral margin posterior to the M_2 is more abrupt than in Stroph or Protophanes, but not as angular as in Protophanes.

FIGURE 44.

Figs. 23A,B, 73, Table 75

Referred material. FISH 10714, right mand with C_1 , P_2 - P_4 .

Locality. Eden Formation, Riverside County, California.

Age. Late Miocene.

Description. The mand is poorly preserved and the teeth are badly broken. The dentary is somewhat laterally compressed, with a shallow intercal groove. P_1 is single-rooted. P_2 is double-rooted, anteroposteriorly compressed, with a tall, anteriorly skewed main cusp. P_3 is anteroposteriorly compressed. M_2 has the trigonid much taller than the talonid. The paracard and antecard are apparently separated by a deep valley.

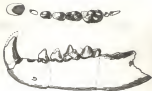
Comparison. This specimen is referred to Protophanes because of the anteroposterior compression and tall cusps of the P_2 and P_3 . This is the earliest record of Protophanes. It is similar in size to recent Protophanes, lyonsi and is smaller than Protophanes montanensis (Barnes) from the early Miocene burned fauna of Kansas. The P_1 , although single-rooted, is relatively larger than in recent Protophanes. The other premaxillae are also set as reduced, thus giving the fish Protophanes a relatively long tooth row.

Figure 27: Ussuri 19-, Throgsson 19-, and cf. Parvulus 19-
Ussuri 19-, IF 11930, right mandible with P_{2-4} ; (A) occlusal view, stereopair (a 1), (C) external view (a 1)
Throgsson 19-, F.A.M. 10114, right ramus with S_1 , P_2 / P_3 ; (B) occlusal view, stereopair (a 1), (D) lateral view (a 1); cf. Parvulus 19-, (E) F-AM 10074, right ramus with P_{2-4} ; external view (a 1).



Figure B2. *Thryomanes* sp. δ_1 in solid, right vertex with δ_1 .

δ_2 - δ_1 , occlusal and labial views (a 2, reversed)



Threat up
Fig. 26a,c, table 21

Isolated material. Of 1928, right mandible with P_2 - P_4 ,
of 1923, left M_2 .

Locality. Bone Valley Formation, Polk County, Florida.

Age. Late Miocene.

Description. The teeth, especially P_4 , are worn. P_2 and P_3 are small and narrow, broader posteriorly, and have short posterior heels. P_3 has a very small anterior angular cusp. P_4 has a narrow posterio-internal cusp/heel and a small anterior angular cusp. The mesosteric fossa is deep and has a wide ventral shelf. The angular process is broad and does not extend from the ventral surface of the mandible. The transition from the horizontal along the ventral margin of the mandible posterior to the M_2 is smooth.

An isolated M_2 from another(?) locality is similar in morphology to that of Isotriaena or Isotria.

Comparisons. The mandible is referred to Isotria because of the low, small, narrow P_2 and P_3 and because of the shape of the angular process. Delquist (1970) described Isotria propinqua from the early Pliocene tooth bank local fauna of Texas. According to Delquist, this form differs from the recent Isotria arizonae in having a narrow posterior shelf and in having a large posterior accessory cusp. Although greatly worn, the P_4 of the Bone Valley Isotria seems to agree with I. propinqua in these characters. However, the P_4 of both Isotria and Isotriaena is highly variable, especially from different

geographic localities, and more material is needed before a specific assignment for the Bone Valley *Phagus* can be made.

Phryganista gen. et sp. indet.

Referred material. TM 58, right δ^1 .

Stratigraphy. Osprey River, Polk County, Florida.

Age. Barstovian.

Description. The tooth is low crowned, with well developed internal and external cingula. The paracase and metacone are united by a neck. A mesostyle is on the labial border close to the paracase. The postacase is large, with preprotocrista and postprotocrista, and connects to the paracase and metacone. The hypocase is a reduced postero-internal swelling of the internal cingulum. The space between the postacase and internal cingulum is united transversely. (Length? 2, width? 1.)

Discussion and comparison. This tooth was found in place in the Bone Valley by John Kirkup with an associated fauna that indicated a Barstovian age for this specimen. It is tentatively referred to the *Phryganista* because of the internal and external cingula and the reduced postero-internally placed hypocase. It would seem possible to derive this tooth from that of *Phryganista* or from that of a form similar to *Phryganista* *viridis*. The Bone Valley specimen is smaller, lower crowned, and has a more robust hypocase than *P. viridis*. In fact, the δ^1 of *Phryganista* could be derived from a form similar to the Bone Valley specimen. Both are low crowned and

less reduced hypostomes. A mesostyle and arched organ) are sometimes present in the δ^1 of *Parasynsotis*. *Parasynsotis* is derived in its reduction of the internal complex and presence of a subacromia.

Issues in Freycinetia Relationships

Cladistic analysis is a logical method for investigating relationships of character states and formulating hypotheses of phylogenetic relationships among different taxa. A cladogram of the *Freycinetidae* discussed in this paper is given in Figure 24. A major difficulty in constructing this cladogram has been in the determination of the polarity (i.e., whether a character state is primitive or derived for the taxon under consideration) of some of the characters used to interpret relationships of the *Freycinetidae*. The accuracy of any cladogram depends on the correct determination of what characters are primitive, which are shared derived, and which have evolved in parallel. If the polarity of a character is misinterpreted, taxon can be falsely allied on shared primitive characters and phylogenetic relationships will be misinterpreted. The fossil *Freycinetidae* are a difficult group to analyze because of their still rather incomplete fossil record, the lack of good cranial material, and, in many cases, even the lack of association of upper teeth with lower or vice versa. In the discussion that follows some of these difficulties will be pointed out and alternative explanations given. Even so, enough characters have been analyzed

Figure 3L. Cladogram of proposed relationships within the *Pratyginidae*. Characters indicated at numbered nodes are discussed in the body of the text.

in the several cases now available that the relationships expressed in Figure 24 are very probably correct.

In order to determine polarities within the Procyonidae it is necessary to find their outgroup, a primitive sister group, within the Procyonidae and closely related families. Ever since Gervais and Reithen (1895) assumed the derivation of Procyon to that of the Arctoidae genus Phlogocyon, many North American and British workers have derived the Procyonidae from the ctenarchine Canidae. Following Rehn (1932, 1941), Simpson (1945) recognized the Ctenarchinae as primitive Procyonidae and included two ctenarchine genera, Phlogocyon and Allogocyon within the Procyonidae. Cain (1946) and Mough (1950) demonstrated the exact structure of the relationship of the ctenarchines and excluded them from procyonid ancestry. Dental resemblances between the ctenarchines and the procyonines are a result of convergence in adapting to an omnivorous diet from a carnivorous one. Fundamental skull dental characters of the ctenarchines include presence of a large hypsacanth on the upper molars and an M_2 .

Telford (1956) reintroduced Flower's (1899) usage of the Arctoidae for the zoogeographic infraclass containing the Ursidae, Procyonidae, and Mustelidae, plus the Viverridae and Huididae. The infraclass Canidae contains only the Canidae. The immediate sister groups of the Procyonidae are within the Arctoidae and it is to them that we must look to interpret what characters are primitive and derived within the Procyonidae, in order to better interpret the polarity of some of the characters of the fossils.

described above. Mitchell and Tedford (1973, pp. 244-247) summarize the basic features of the Elipsocera Curidae, Mutillidae, Encidae and Procyonidae. Elipsocera, described above, has a typical procyonid ear structure. Elipsocera and early Procyon genera which have procyonid-type ear vesicles are Elipsocera, Elipsocula, Encidulus, Encidius, and Gimnecrallia. John (1958) described Encidius and Gimnecrallia from the early Eudipterian Viatkiniell-Host fauna of Germany as self-fertile wasps. Saunders (1944b) included Encycyon and Alloprocyon as close relatives of the two Eudipterian genera within the Mutillidae. After a detailed examination and comparison of the ear region of Gimnecrallia, Encidius, Elipsocula, Encidulus, Encidius, and E. punctatus, Saunders (1945) concluded that these genera were Procyonidae and that Alloprocyon, Alloprocyon, and Encycyon could also be included in this family. Whetstone (1949) included the latter two genera in the Encidae.

It is beyond the scope of this paper to sort out the phylogenetic relationships of the above genera. This would require interpretation of the polarities of arched structural characters. According to Hunt (1974, 1977), the Type A bulla of wasps, anthomyiids, Elipsocera, and certain wasps is primitive not only for the Encidae, but for the Curimora. The type A bulla is uninflected and has a large ectotympanic and small antitympanic(s). Hunt states that inflation of the bulla, chiefly by expansion of the antitympanic, occurred independently in the Elipsocera, Encidae, Procyonidae, Mutillidae, and other Mutillidae. This character distribution suggests that the Type A bulla may not be primitive

for the Carabidae. Several types of modified carabid bullae are first found in the early Stenopodae. A greatly enlarged sclerite which has not been rigorously described is believed to be primitive. The propodeal-type ear region may in fact be primitive for some arctoids (Lafont, 1919a, pers. obs.). Nevertheless, these primitive arctoid genera discussed above, as well as others, served as the outgroup comparison of the genera described in this paper. Besides having a propodeal-type ear region, these genera have lost the stiphonoid canal and R_3 .

The recent genus *Pezomachus* is usually classified in the Procyoninae and is often compared with *Amantia* (Dough, 1944). Both genera are arboreal dung-feeders that often travel together in the same bands, and externally are physically similar. *Pezomachus* is much more specialized dentally, cranially and postcranially than *Amantia*. Its ear region is unlike that of any other procyonine (Sagall, 1942). Features such as the elongated pronotum, P_4 taller than R_4 , and P^1 with laterally placed protuberance may place *Pezomachus* among the non-basitarsine procyonines treated here, or more likely they are parallel characters in this highly specialized genus. Sagall (1942, p. 52) discusses several metailid-like features of the auditory region of *Pezomachus* and concludes that "*Pezomachus* may perhaps be regarded as a marginal member of the metailid stock that has retained certain characters from the common arctoid ancestry." *Pezomachus* has long been recognized by some authorities as distinct from other living Procyonidae (e.g., Pocock, 1921; Simpson, 1945).

Brachiodia and Leptostegopsis, in particular, appear to form the sister group[1a] of the higher Procyonidae. Characters which unite all these genera in a monophyletic taxon distinct from other archbats are [Figure 1b; branch point 1]

- (A) R_2^2 enlarged
- (B) P^2 with protocone slightly more posteriorly, a posterio-internal cingulum and a hypocone
- (C) R^3 with hypocone reduced to a circular cusp

When Hildegarde (1948) described Leptostegopsis poliolepisensis from the late Neogene/Quaternary Pahrump local fauna (part of the Barkerville fauna from the lower part of the Flaming Formation, San Jacinto County, Texas), he speculated that "the size and of its characters preserved would place it in a central primitive position within the procyonids and with certain resemblances to the canids" (p. 500). Canid resemblances are similar to those discussed concerning Phlogothys and other Canarionae. Leptostegopsis 11 does seem to be the primitive sister group to the non-canarionine procyonines. Characters which unite these higher procyonines (branch point 2) are

- (A) P^2 with enlarged protocone
- (B) R^2 and R^3 with strong proprotoconids and mesoprotoconids and strong internal cingulum
- (C) protoconids elongate
- (D) M_1 with paracond and metacond close together
- (E) palatines expanded posteriorly
- (F) M_2 with trigonid reduced in height relative to P_2

(X) ectopneustic enlarged

(Y) prefrontal process in contact with buftia.

Although the P_1 of *Monocorynus* linked to *E. primitivissima* is unknown, the structure of the P^1 , with its large, relatively uniformly placed prebasal, indicates that the pericordal was probably close to the subcordal, making the trigonal less Wade-like than in *Basariscus*, *Isotriax*, or primitive acrobids.

Monocorynus *legion* from the Montserrat Formation is one of the earliest known Progonitidae from North America. A slightly earlier occurrence may be *Basariscus* sp. from the 'Lower Harrison,' possibly Harland Formation equivalent, of Nebraska (Cook and Randewald, 1962). The specimen is badly damaged, and is described but not illustrated. This specimen, Abel 1003 (Formerly 8028) is reported to have a double-rooted P_1 , but examination shows that the P_1 is single-rooted (R. Gaffney, pers. comm.). The Progonitidae appear to be Osmingtonian anapneustic from Canada.

Characters (X) through (Y) may instead be applicable at branch point 3 or 4. Prefrontal in contact with frontal and expanded palpus also characterize *Alchora* and the Uronei. If prefrontal-frontal contact is primitive for the acrobids, non-contact is derived for *Basariscus*. Posterior palpal expansion appears to be independently derived. In *Asphygodesmus* there is little expansion. In *Alchora* and Uronei the palpus terminates with a concave border, in the Progonitidae there is a median spine.

There is only a small amount of morphologic difference between the external bones of Alphacodon goldblumensis and E. lachry. The characters distinguishing E. goldblumensis, however, are derived characters shared with the other higher Plesiosauroidea. This makes Alphacodon, as here recognized, a paraphyletic taxon. The dental differences between these two fossil species are approximately equivalent to those between the two Recent species Stenacodon (Stenacodon) atlantic and Stenacodon (Centronia) sumatrensis, which some systematists recognize as distinct genera. However, the amount of difference between these two species is much less than that between most species in the monophyletic genus Stenacodon. Huxley (1945, p. 238) noted that "bringing things together properly is the more useful and important function of taxonomy."

There is no a priori reason why paraphyletic taxa should all be allowed. In fact, they may reflect biological relationships such as adaptive radiations or even ancestral descendant lineages better than can be done within the strictly logical framework of cladistic taxonomy.

The synapomorphies for branch point 3 are

- (A) P^4 with small penultimate
- (B) P^4 with reduced reticulate blade
- (C) P^3 with more posteriorly placed preblades.

The characters at branch point 4 are somewhat tenuous because of the lack of upper dentitions of Lichacodon, and the poor quality of the material of Lophocetus available to us. Branch point 5 may in fact be an unresolved trichotomy. Characters which seem to

with these part-heterodontid frequencies are [branch point 4]

- (A) P^3 with paracids longer than anterior
- (B) P^3 with paracids not sloped posteriorly

Branch point 5 unites Synsaurus with Archaeosaurus. Synsaurus is known from the Hupeyuan or Montanaroceras [late Miocene] to Chapadmalal [Pliocene] of Argentina (Berta and Marshall, 1978). It is the latest well fragment in South America from North America (Patterson and Jassby, 1972). There is still a large time gap between the appearance of Synsaurus in South America (latest Miocene) and the probable time differentiation from the hypothetical common ancestor of it and Archaeosaurus (early Eocene) - however, at least it is now possible to relate Synsaurus to a North American sister group.

Characters which unite Synsaurus with Archaeosaurus are [branch point 5]

- (A) P_1 with reduced paracoid
- (B) P_1 with well developed separate subcaudal
- (C) P^3 with reduced hypocaud
- (D) P^3 with paracaud placed more posteriorly
- (E) P^3 with loss of paracaud-antecaud blade
- (F) mastoid process broadened
- (G) frontal sinuses greatly enlarged
- (H) preglenoid process present

Character (E) may be in doubt since no known P^3 's of Synsaurus were available and illustrations had to be relied upon. Characters

(F), (G), and (H) may be related to the large size of the specimen of *Opomys arizonae* and *Arizonops fricki*. Synapomorphies for *Opomys* (branch point 5) include reduced premaxilla, absence of a hypocone on the upper molars, and M_2 with anticonoid smaller than protoconoid. *Arizonops* (branch point 7) is distinguished chiefly by the great reduction of the anticonoid on M^3 and greater approximation of the paraconoid and anticonoid on M_2 .

Branch point 8 is tenuous because the upper dentition of *Lithomys* is unknown. *Lithomys* has many primitive higher primate characters. Possible synapomorphies linking it with the *Reithrognathus* group are

- (I) M_2 with wide talonid
- (J) M_2 with anticonoid and entononoid close together
- (K) alveolar sulci fairly wide
- (L) M^{1+2} with reduced internal cuspules

The placement of characters (I) and (L) depends on the placement of the recent genus *Agoutiomyia*. These are characters which unite *Reithrognathus* with *Peromyscus*, *Reith*, and *Procyon*, and hold at branch point 8 only if *Agoutiomyia* and *Lithomys* are sister groups. A character which seems to unite these two genera, but which is difficult to analyze because of homology to *Lithomys*, is enlargement of M_2^2 relative to M_2^3 (branch point 10).

Characters which unite *Peromyscus*, *Reith*, and *Procyon* (branch point 11) are

- (A) Angular process above level of mesiodistal tooth row
- (B) M^3 with distinct anticonoids posterior to protocone
- (C) M_2 enlarged

Fraxinus is unusual in that it has large double-rooted P_1 's, a rarity in the Carpinaceae. Among living carpinaceae, Bassia has small double-rooted P_1 's and Asparagopsis occasionally has them. A double-rooted P_1 , then, may be a synapomorphy for branch point 8 or 10. On the other hand, both Fraxinus (Olsen, 1960) and Alnus (Olmstead, 1974a) can have double-rooted P_1 's, which may mean that this is primitive for the Fraxinoideae. Later definitions of Alnus would help resolve this problem.

Characters uniting Fraxinus and Bassia in earlier trees are (branch point 15)

- (A) loss of external cingula on π^{1-2}
- (F) π^1 with anterior-reticulate area
- (G) P_{1-2}^{1-2} reticulate
- (2) long septum extending to root of secondary apices.

The reticulate of π^1 of Fraxinus and Bassia is sometimes interpreted as a hypocostae. This may have been brought about as a result of comparing the π^1 of these two genera to that of Opuntia, which do have a prominent hypocostae. Comparison of Fraxinus, Bassia and Opuntia demonstrates that this costae is a postero-laterally placed reticulate which is connected to the protocostae by a short postreticulate. The single-rooted P_1 and compressed P_{1-2}^{1-2} of Fraxinus are derived characters related to shortening of the face in this genus.

The cladistic analysis shows that Fraxinus and Bassia are more closely related to each other than either is to any other analyzed. The two genera probably differentiated from each other sometime

during the Mesozoic, with the first probable record of such genus in the late Mesozoic. Basimarginis, the latest South and Central American ooligo, has no fossil record. It is tentatively placed in the cladozoan, but it is more closely related to Argus, Protargus, Argonema and Ligustrum than it is to other procyonids.

Family Gasteridae

Genus Argonema

Argonema. In 1886, Joseph Leidy, the father of North American vertebrate paleontology, described material collected from the fossil beds along the Missouri River in north-central Nebraska. The fossils were collected the year before by Dr. Ferdinand Vandevert Hayden, the paleontologist with the Verneen expedition which was exploring the region between the Platte River and the Black Hills (Leidy, 1886). Among the 28 new species and 13 new genera and subgenera Leidy described were the following three taxa of corals (in order of description): Corals Argonema, known from a lower jaw with a worn P_{2-4} and roots of the premolars; Corals (Argonema) argenteum, from a large jaw fragment with P_{2-4} , P_{7-8} and Argonema form, known from an uncoral, isolated P^d . The material was later figured by Leidy (1886) and reillustrated in Henderson and Gregory (1940). Leidy (1886) was unsure whether Argonema form was a coroid or a Felid because, although it had wolf-like proportions, it also had an anterior accessory cusp, a parastyle, that is characteristic of canis. He thought, however, that it might belong to Canis (Argonema)

bayleri. Cope (1861) was able to conclusively demonstrate that delarum form was a subspecies and considered it to be a junior synonym of delarum, as did Bates and Shown (1890), who also included delarum in this genus. Matthews and Sturges (1930), on the other hand, thought that delarum agreed better to class with bayleri. Vanderhoof and Gregory (1940) considered delarum to be specifically indeterminate.

The generic name delarum has been applied to the hylomys, Clarendonian and early Neopitilian primitive hyssopine-like dogs of North America. Within the genus delarum are two distinct species groups (Pollock, 1944; Brady, 1954). The delarum bayleri species group, including delarum, delarum, delarum, delarum, and delarum (delarum), is characterized by inflated premaxilla with narrow rostrary cusp, P_1^1 with a narrow hypocostal, P_1 with reduced antecostal and antecostal, and P_2 with enlarged postcostal. The delarum delarum group, which includes the following named species: delarum, delarum, delarum, delarum, delarum, delarum, delarum, delarum, and delarum, has reduced P_1 - P_2 , P_1 with antecostal equal to hypocostal, P_1 enlarged, and P_2 with widened postcostal, antecostal and ischial. Tedford and Frasier (1955) formally recognized the generic distinction between the two species groups by resurrecting the generic name Prohyssopus in a discussion of the Neopitilian canids. Schlosser (1957) had applied the name Prohyssopus to delarum, believing it to represent a true North American hyssopid. In using Prohyssopus for the bayleri species group, Tedford and Frasier (1955) imply

that the parvus group is conspecific with Helicodon formos, an assumption also proposed by Moody (1964).

In the fresh collection of the American Museum of Natural History (F.A.H.), there are large samples of these primitive iguana-like lizards, including many associated skulls and jaws. This permitted easy and accurate identification of the upper and lower dentitions of the two species groups.

The P^A of Helicodon 1-3, (including both the boonensis and parvus species groups) is somewhat variable in degree of inflation of orbits, height of crown and relationship of length of premaxilla to length of maxilla. One feature by which the P^A of members of the gambusia group can be distinguished from that of the parvus group is the structure of the premaxilla and its relationship to the parastyle and premaxilla. In Helicodon formos (Fig. 25) the premaxilla is separated from the parastyle by a valley. The premaxilla and premaxilla are connected by a ridge. The premaxilla has two cusps at this ridge: a large posterolateral cusp and a small posteromedial one. This separation of the premaxilla and parastyle is always observed in members of the gambusia group (e.g., Patterson and Giffley, 1964, Fig. 3a, 3b, 3c, 3d, 3e, fig. 6). A good which can be used between the P^A of gambusia and the P^A 's of members of the gambusia group from Guatemala and Subtropical Americas in the F.A.H. collection is the parvus group (Fig. 25) the premaxilla is connected to the parastyle. The premaxilla is a large anteromedial cusp (Patterson and Giffley, 1964, fig. 3a). In Guatemalan members of the parvus group from California the premaxilla-parastyle connection is sometimes

Figure 25. σ^0 of Aglycydon and Epilcyon. Left, Aglycydon terre
 USNM 523, paratype, occlusal view (x 2.5).
 Right, Epilcyon cf. gambel, UP 24475, from the Lower
 Bone bed, occlusal view (x 2.0).



not very strong, but these P^A 's can be distinguished from that of *E. ferox* by their weaker parastyle. In any event, members of the *sericeus* group first appear in the plains in the Cretaceous (Tedford et al., in press) and specimens in the collections of the AMNH have a strong parastyle-protostyle connection. The group *delacourae* should therefore be restricted to members of the *laetitia* group. *Ergaticus* Leidy, 1850, has priority for members of the *sericeus* group.

delacourae and *Ergaticus* may partially represent separate lineages from *gambelii* (a definition, written down). *delacourae* became extinct at the end of the Cretaceous (Tedford et al., in press). *Ergaticus* is present in very early Miophilian faunas of the plains where it is represented by the large species, *Ergaticus pallidus*. *delacourae*, the characteristic Miophilian bone-crushing dog, evolved from a smaller species of *Ergaticus*.

Woodward and Gregory (1900) and Macdonald (1946) derived *delacourae* directly from *gambelii*. Macdonald (1946, p. 61) characterized the *delacourae* lineage as "a line of short-faced hound dogs." *delacourae*, e.g., the *laetitia* species group (Peters, 1944) is probably a separate lineage from *Ergaticus* and is not ancestral to *delacourae*. *Ergaticus*, formerly the *sericeus* group of *delacourae*, which includes species that were placed in *syntherion*, is ancestral to *delacourae*. Derived characters *Ergaticus* shares with *delacourae* include shortening of the face, sloping of the frontals, broadening of the palate between the caniniforms, enlarging of the P_4 , and having a protocune-parastyle connection on P^A . Macdonald (1946, p. 61) notes this connection in the description of *E.*

sublingual and illustrates it. In contrast to this with the premaxilla-maxilla connection in Foranodon hemionodon (see Antrodont), the connections are mutually associated. Antrodont is derived from gigant by further reducing and simplifying P_{1-2}^{1-2} , enlarging P_4^4 , and further during the frontal bones of the skull.

Epigen of - genus (Lepid)

Figs. 25, 26; Table 22

Material Material: BP nos. 24123-24125, left mand; 24026-24028, right mand; 24029-24030, P_1^1 ; 24126-24128, P_2^2 ; 24129-24130, P_4^4 ; 24027-24028, K_1 ; 24126-24127, 24030, lateral fragments, all from the Lower Bone Bed, Jackson County, Florida, latest Cretaceous Land Mammal Age.

Description: The P^2 is much larger than P^1 or P^3 . In BP 24126, the palate of an old individual, the right canine is missing and the alveolus resorbed, reflecting survival of this individual after loss of this tooth. P^1 is single-rooted, P^2 is double-rooted. The main cusp is large and anteriorly placed. There is no anterior accessory cusp. The posterior accessory cusp is in the posterior flank of the main cusp. The posterior cingulum is well developed and may have a posterior cingular cusp.

The P^3 has a small anterior accessory cusp. The posterior accessory cusp is separated from the main cusp by a narrow slit. A posterior cingular cusp is usually present on the posterior cingulum. The rootlet is resorbed at the level of the posterior end of the P^3 , giving this tooth a sigmoid appearance in some specimens.

Figure 10. Decomposition. (A) of 24520, left $P^2 \cdot d^2$,
 occluded view (x 1.5); (B) of 24452, left satellite
 with t_1 , $P_2 \cdot d_1$ (x 0.5); (C) of 24571, left satellite
 with $P_2 \cdot d_2$ (x 0.5).



A



B



C

Figure 27. Figure 47 - Section. (A) of 26119, (B) of 26120, (C) of 26120, (D) of 26120, right mandibles (x 0.1).



Table 23. Measurements taken on *Erigeron* cf. *interrus*.

	N	\bar{X}	S.D.	CV
P^R length	75	25.42(5).870	21.1-36.5	5.5
width	75	12.29(5).267	10.0-14.7	4.7
P_1 length	75	17.36(5).273	15.2-19.8	4.3
width	75	10.00(5).200	8.8-10.4	4.4
P_2 length	8	8.73(4).121	7.0-9.8	7.2
width	8	4.60(3).166	4.2-6.0	7.7
P_3 length	9	10.00(5).176	10.0-12.8	4.8
width	9	5.77(3).154	5.4-7.5	4.6
P_4 length	20	17.02(4).265	16.0-19.7	4.3
width	20	9.02(3).173	8.0-10.4	5.5
P_5 length	30	20.17(4).234	20.0-21.8	4.4
width	30	11.80(3).153	10.0-13.5	5.3
P_3-P_2 length	7	16.16(3).308	13.0-19.7	4.8

The P^4 has a well developed protocone and paracone. In little more specimens the paracone is connected to the protocone by a double set of ridges. The metacone has a well developed internal cuspular.

The P^3 has the protocone larger and taller than the metacone. The metacone is slightly smaller than and is connected to the protocone. The internal cuspular is continuous with the preprotoconids and the postprotoconulocrista. A short, variously developed anterior cuspular is present at the base of the protocone. A small paracone is present. The apocrista is broad and in two of the specimens is bifurcated.

The P^2 is smaller and the cusps are much lower than in the P^3 . In four specimens the tooth is double-rooted. In some it is three-rooted.

The lower premolars are highly variable in size, shape and degree of development of accessory cusps. The P_1 is single-rooted and small. P_2 is double-rooted. Most specimens have a posterior accessory cusp. About one-half have an anterior cuspular cusp. A small anterior cuspular cusp is present in approximately half the specimens. In some jaws, particularly the larger specimens, the P_2 is skewed, with the anterior root external to the posterior root and the posterior root overlapping the anterior root of P_1 . This condition is also present in some of the average-sized specimens.

P_3 is larger than P_2 . A posterior accessory and posterior cuspular cusp are always present. The apocrista projects an anterior

circular cusp. P_3 may also be offset to the jaw, but not as much as P_2 .

P_4 has a prominent posterior accessory cusp that is separated from the main cusp by a notch. The notch is widest laterally opposite the junction of these two cusps. The posterior cingulum is well developed and terminates with a posterior circular cusp. Two specimens possess an anterior accessory cusp that is better developed than that on the P_4 of the holotype of *G. jaffaga*. A poorly developed anterior accessory cusp is present in five specimens. It is absent in 13 specimens.

P_5 is a robust tooth with a prominent protoconid and paraconid. The metaconid is variably developed. In all specimens it is a short cusp, but in some it is only poorly developed. The talonid is narrower than the trigonid. The hypoconid and entoconid are subequal in size and are connected by a cross creel. A small cusp may be developed between the protoconid and hypoconid.

P_6 has a trigonid with subequal protoconid, paraconid and metaconid, and a long narrow talonid.

P_7 is single-rooted.

Glossodon cf. *laevis* (Gidley)

Fig. 32, Table 23

Differential diagnosis.— UF nos. 25421, 25422, P_4 , 25550, M_1 , 24524, mandible fragment with M_2 ; 25570, mandible with broken P_4 - M_1 , all from the Love Bone Bed, Alachua County, Florida. Latest Claibornean Land Mammal Age.

Figure 18. Figure 18 of Figure 18. Of 24478, sectional and external view (x 1.42).



Table 23. Measurements taken on *Eucema cf. longhorn*.

	n	\bar{x}	S.E.
P_2 length	2	29.19	21.2-32.5
width	2	12.59	11.8-13.4
P_3 length	3	30.33	29.6-34.8
width	3	13.32	12.2-14.3
P_2-P_3	1		(86-9)

Description. The mandible (JF 24570) is massive, with a heavy chin. P_2 and P_3 are set obliquely in the jaw. P_4 and P_5 are similar to those of *L. cf. sargus*. The anterovent of P_5 is very weak.

Discussion. The following species should have been proposed for synonymy of *[Glyptotus]* *L. sargus* (Leidy, 1854): *L. inflatus* (Fosterhoef and Gregory, 1940), *L. sublaevis* (Reidy, 1940), *L. haydeni* (Leidy, 1858), *L. mortimeri* (Clark, 1914), *L. retusus* (Matthew and Cook, 1908), *L. spinosus* (Overman, 1914), *L. transmontanus* (Stanton and Fosterhoef, 1940), and *L. [lignocollis]* (Fosterhoef, 1931).

[Glyptotus] sargus was described by Leidy (1854) as *Glyptotus sargus*. The holotype, a lower jaw with a worn P_{5-2} and roots of the premolars, was collected by F. F. Hayden in the valley of the Nebraska River. Cope (1881) referred this specimen to *Salicodon* and *Achuradon* on the basis of a nearly complete skeleton with skull from Croftwood Creek, Hitchcock County, Nebraska, of probable Claibornian age, this he referred to *L. sargus*. This material was later figured in Cope and Matthew (1875), helping to make this species central to the concept of what was previously believed to be represented by *Salicodon*. A revised diagnosis of this species and an illustration of the holotype are given by Fosterhoef and Gregory (1940).

The goniatitic species, *[Glyptotus] haydeni*, was also collected by Hayden from the valley of the Nebraska River and described by Leidy (1858) as *Glyptotus (Salicodon) haydeni*. It is between the descriptions of *L. sargus* and *L. fursi*. The Nebraska River fauna comes from the lower members of the Valentine Formation and is late Mazonian in age (Webb, 1959a). The above three species are sometimes assigned

is belong to the Tennesse River fauna. Other faunas have been collected from the valley of the Tennesse River, notably the early Clarendonian Barge fauna from the upper part of the Silurian Formation and the middle Clarendonian Ponce de Leon fauna from the top back member of the Ash Hill Formation (Webb, 1961). Since the earliest time referable to *Erygmus* in this region is the extensive collection of the Petric Laboratory After First appear in the base of the Ash Hill Formation (Clifford et al., in press), it is reasonable to assume that the holotypes of *E. hypoleus* and *E. agassiz* are from this formation.

Erygmus affinis was described by Vanderhoof and Gregory (1961) as *Arcturiscus affinis* from the Clarendonian Fly Spring local fauna of South Dakota. They hypothesized that it was a direct descendant of *E. agassiz* and distinguished it by its larger size and its wide inflated promerula and carapaculum. Since it was known only from the holotype, they made no investigation of the range of variation of size and inflation of teeth within both species.

Erygmus validus was originally described as the subgenus *Beloriscus* *hypoleus validus* from the upper Snake Creek fauna of Nevada (Matthew and Cook, 1938). Sinner, Sinner and Gooris (1957) tentatively refer the type specimen to the early Mesozoic *Erygmus* fauna from the Johnson member of the Snake Creek Formation. This tooth was distinguished from *E. hypoleus* principally by its shorter, more rounded promerula region. Burton and Vanderhoof

(1933, p. 179) noted that Aclerodes Haydeni Walden, "is almost certainly not Aclerodes, because of the greatly shortened premaxillary space with its transversely set alveoli." Johnston (1936) and Ross (1948) referred the holotype and material from the early Devonian (Sagami local fauna of Tazew to Onychodonta Walden. Ellis (1957) has noted that the degree of crowding, the specific character supposedly distinguishing O. Walden, cannot be determined in the holotype of O. Haydeni, since the teeth anterior to the P_3 are missing. Crowding not crowding of the premaxilla is an extremely variable character in Aclerodes and Onychodonta. Wilson et al. (1977) place this species in Aclerodes.

Onychodonta Walden was described from the upper portion of the Nevada Formation, California (Walden, 1919) as Aclerodes? Walden. This type specimen is an upper jaw fragment with P^3 , P^{3+2} and a portion of the P^2 . The P^2 has a broad posterior end and the P^3 appears to have posteriorly connected to premaxilla. Initialing this specimen is better assigned to Onychodonta. Artzner (1979) regarded O. Walden to be closely related to, and possibly a subspecies of, O. Haydeni. Stock (1984) described a lower jaw from the Nevada Formation which he referred to Aclerodes Walden. He noted the similarity of this jaw to the holotypes of O. Haydeni and O. Haydeni Walden. Stock and Ruedemann (1980) made this jaw the type of Onychodonta Ruedemann. Ross (1948) noted that O. Ruedemann is closer in size and detail to O. Walden, but can be distinguished from O. Walden in its smaller size and more reduced premaxilla. Ruedemann (1948a) referred two jaws from the late Devonian Black Rock Ranch local

fauna of California to *Helicopsis scholzei*. These jaws belong to a species of *Helicopsis* (sensu stricto), not *Helicops* *scholzei*. The Ricardo mandible described by Stock is conspecific with the holotype of *Helicops scholzei*, for exactly the same reasons that Brits (1986) synonymized *E. concoloratus* with *E. delany*.

Stock (1984) described *Helicopsis mortifer* from the Snake Creek beds of Nebraska. Skinner et al. (1987) interpreted that the holotype came from the late Cretaceous-latemost member of the Snake Creek formation. Lockwood and Gregory (1940) synonymized *E. mortifer* with *E. huxleyi*, stating that it agreed more in size with *E. huxleyi* than with *E. jaynesi*. Brown (1944) felt that the holotype of *E. mortifer* was within the range of variation of *E. jaynesi*, especially for a late occurring member of that species. Brits (1986) recognized both *E. mortifer* and *E. scholzei* in the earliest Neogene(?) Ansett local fauna of Nebraska. He distinguished *E. mortifer* by its slightly smaller size and more sparse punctation. Brits doubted the synonymy of *E. mortifer* and *E. jaynesi*. Skinner et al. (1987) agreed that this distinction should be maintained until a complete investigation of the specimens in the extensive collection of the Field Laboratory AMNH could be made.

Helicops littoralis is known from a skull from the upper Miocene marine Santa Monica Formation of Cracker Springs, California (Benderhoof, 1931). These deposits are equivalent in age to Cretaceous terrestrial deposits (Graham, Jones and Savage, 1984; Tedford et al., in press). Originally described as a species of

Eggenopsis. It was later transferred to the new genus Schuchertella (Stanton and Sanderson, 1960).

Schuchertella schucherti was described from the late Clarendonian Flack Rock Beach local fauna of California as a species of Orthis (Oriskany, 1938). Additional material was described and illustrated by McDonald (1964). Becker distinguished S. schucherti from species of Schuchertella principally on the well developed accessory cusp on the P_1 and the elongate P_2 . These characters and others, including relatively unadorned P_{1-2} with accessory cusps and small P_4 with prominent posterior accessory cusp, indicate that this species is referable to Eggenopsis. S. littorata, which is somewhat less derived than S. schucherti (McDonald, 1964), is also referable to this genus.

McGrew (1968) made a morphometric study of seven specimens of Eggenopsis from Clarendonian deposits of Nebraska and South Dakota. He concluded that S. eggeni represented a chronocline that increased in size through time and synchronized S. inflata and S. merittii with S. eggeni, considering them to be middle and end points, respectively, of the S. eggeni chronocline. McGrew interpreted the Holman River locality for the holotypes of S. eggeni and S. inflata as indicating that these two specimens were of late Tertiary age. Tafted et al- (in press) have pointed out that Eggenopsis first appears in the Great Plains in the Clarendonian Ash Hollow Formation. Landy's two holotypes are probably from the lower member, the middle Clarendonian Cap Rock Member, which has produced the well-known *Strophodontella* fauna (Webb, 1966). Nevertheless, there is

a general tendency towards increased size in *Euscyops* from the late Eocene through the early Miocene is exemplified with good stratigraphic control in the *E. m.* collections (Trigs. 35, 36).

Holmes (1944) interpreted from Leidy's descriptions and the preservation of the specimens that the holotype of *E. haydeni* and *E. parvus* were found in the same deposit. Because of the great difference in size of the two holotypes, he stated that they were valid, distinct species. He felt that the holotype of *E. mortifer* was within the range of variation of *E. parvus*, especially for a late occurring member of that species. Roodhouse and Gregory (1940) had synonymized *E. mortifer* with *E. haydeni*, stating that it was much nearer in size to *E. haydeni* than to *E. parvus*. Citta (1958) distinguished two species of homophagines from the early Miocene Ansett local fauna of Victoria. He referred the largest specimen to *Homophagus (Euscyops) validus* and referred the six other specimens to *Homophagus (Euscyops) cf. mortifer*.

Citta (1958) doubted the synonymy of *E. haydeni* and *E. mortifer*. Skinner et al. (1970) agreed that this distinction should be maintained until a complete investigation of the extensive collection of *E. m.* specimens could be made. Citta (1969) did not distinguish between *E. haydeni* and *E. validus* and used both terms, apparently interchangeably. He noted that the diagnostic character of *E. validus*, the crossing of the precolars, cannot be observed in the holotype of *E. haydeni* because the jaw is broken anterior to the P_2 . Citta used *E. validus* for the large homophagines from Higgins and Ansett, following Roodhouse (1940) and Johnston (1956). He stated

Figure 18.: Histograms of N_1 length in samples of glauconite.

- (A) Barlow fauna, late Mesozoic, California;
- (B) Champion fauna, middle Clarendonian, Texas;
- (C) Lepidodermis local fauna, late Clarendonian, Texas;
- (D) Goli local fauna, late Clarendonian, Nebraska;
- (E) Love Bone bed local fauna, latest Clarendonian, Florida; (F) Part of Goli, \pm Frederick local fauna, early Romphillian, Oklahoma; (G) Higgins local fauna, early Romphillian, Texas; (H) Jack Swipes local fauna, middle Romphillian, Kansas.

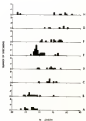


Figure 33. Histogram of P_L-R_L sample in samples of Excerpt.
See Figure 28 for explanation of A-B

that the anterior processes of L. pallidus from these two localities are crowded and slightly transverse in their orientation.

Crowding and transverse orientation of the processes are highly variable characters, as can be seen in the sample of L. cygus from the late local fauna, in which some of the smaller specimens possess effort, overlapping processes. This variability can also be observed in the large L. cygus sample from Part of Entry Pit (Clarendon). At present there is no diagnosis to distinguish L. hughesi, as used for the Clarendonian specimens of large L. cygus, and L. pallidus, as used for the early Mesquithian specimens, if indeed there is a difference between the two. Several problems need to be resolved before the number of species of L. cygus can be determined. Because R. Taylor and E. Tedford of the AMNH are working on a detailed review of all the Mesozoic birds, only a preliminary analysis will be attempted here.

A basic problem is the determination of the number of species of L. cygus present in any one local fauna. In the late Mesozoic faunas local faunas of California a single, possibly sexually dimorphic species (CMB.6 for M_1 length) is probably present. In the white Clarendonian Clarendon fauna of Texas two species are probably present: a large form, L. cf. hughesi, represented by a single specimen, and a small form, L. cf. cygus. L. cf. cygus from the Clarendon is also variable (CMB.6 for M_1 length) and does not show any distinct clustering. The evidence from the late Clarendonian Red and L. pallidus local faunas of Nebraska is more difficult to interpret. When these two samples are combined there

appears to be a more abundant large species, *E.* cf. *lapidus*, and a rarer small species, *E.* cf. *parvus*.

The coefficient of variation for H_L length for all *Eupogon* from the late site is 3.7, which is not much larger than that of the forerun species, which are interpreted above as belonging to a single species. However, there is a marked separation in size between the five large specimens, which are assigned to *E.* cf. *lapidus*, and the smaller more abundant specimens of *E.* cf. *parvus* (CV=4.4). The low overall CV (~3.7) may be an artifact of the small sample size of the large specimens. The H_L lengths of *E.* cf. *parvus* form a bimodal distribution, a peak for the smaller specimens (<30 mm) and a plateau for the larger specimens (>30 mm, >34 mm). These two size classes have means that are statistically different from each other (196.7%, $P<0.001$). This bimodal distribution is continuous, however, and is interpreted as resulting from sexual dimorphism.

The samples from the early Neopliocene Port of Entry Pit (10m01) and 10m02a (lower) are less clustered and have a greater range than the other samples (CV=5.5 and 5.3, respectively, for H_L length). At Port of Entry Pit there is no discrete division into a large *E.* *validus* and a smaller *E. merulifer*, as Kribs (1987) proposed. It seems more likely that there is only a single, highly variable taxon, *E. validus*, present. *Sceloporus*, a smaller, more advanced ophiophagous, is present in the late early Neopliocene Jack Bayre local Fauna of Texas. In this sample *E. validus* has a smaller range of tooth size, a lower coefficient of variation (CV=3.7 for H_L length), and is larger than the other late samples.

A possible explanation of these differences may be sick banding in the absence and character displacement in the presence of a closely related competitor.

As noted above, the prevalence of the holotype of *E. sagrei* is uncertain. Taylor and Seiffert (in preparation) intend to define a Neotypic sample and record the diagnosis of this species. The holotype of *E. sagrei* is approximately the same size as the smallest sample of *E. cf. sagrei* from the lower local fauna. Although the means of specimen measurements of *E. cf. sagrei* from the earliest Clarendonian Clarendon fauna of Texas are smaller than those from the latest Clarendonian lower local fauna, there is considerable overlap between the two sets of measurements. The two samples probably represent a temporal or geographical cline of the same species, *E. sagrei*, such as Hubert (1984) suggested. The morphological differences used to define *E. inflatus* are well within the range of variation seen in *E. cf. sagrei* from the late Cline. Specimens of *E. cf. sagrei* in the lower local fauna (Fig. 37) range from having small flange processes, similar to those of *E. cf. sagrei*, to specimens with inflated processes with accessory cones better developed than those in the holotype of *E. inflatus*. Other described specimens that can be referred to *E. cf. sagrei* include *E. haydeni* and *E. parvus* (Britton and Sealey, 1964) and *E. haydeni* (Smith and Osborn, 1932). The specimen Smith and Osborn (1932) referred to *E. sagrei* is probably referable to *longatus*.

The systematic position of *E. parvulus* cannot be determined until a review of the upper lower Cretaceous is made (Taylor

and Telford, in preparation]. The holotype mandible could either represent a large specimen of L. cf. *parvus* or a small mandible of L. cf. *hypnoid*.

Proteropon cf. *parvobell* Telford and Taylor

Fig. 388, 1

Inferred material: W. no. 15666, right M^1 ; 15671, right M^2 ; 15696, right P_2 ; 15661, 15735, identical jaw fragments, all from the lower Bone Bed, Alachua County, Florida, late Cretaceous (late Maastricht Age).

Description: M^1 . The tooth is externally-inferiorly obovate. The cusps are small. The cingula on the borders of the tooth have beveled enamel. The protocone is connected by a prominent preprotocone to a small parastyle. The external cingulum is well developed, but is restricted medially between the parastyle and metacone. The metacone is especially well developed. It is connected to the external cingulum by a weak posterostegocrista. The hypocone is large and is situated slightly anterior to the metacone and lateral to the protocone. A median notch separates the hypocone from the precingulum. The precingulum and postcingulum are prominent. A weak external cingulum is present on the postero-internal border of the tooth (length 6.2, width 3.6).

M^2 . The tooth is well worn, but the cusps appear to be low crowned. The large protocone is connected to a small metacone. The hypocone is situated on the postero-internal border of the tooth (length 6.8, width 4.1).

Figure 31. Proterocyon cf. modestus, Flamingo sp., and Tithonocoris near T. laeta. (A) Proterocyon cf. modestus, BP 25458, π^3 , occlusal view (x 4). (B) Proterocyon cf. modestus, BP 25458, π^2 , occlusal view (x 4). (C) Flamingo sp., BP 25501, π^3 (x 4). (D and E) Tithonocoris near T. laeta, BP 25453, occlusal and anterior views (x 6.67). (F) Tithonocoris near T. laeta, BP 25458, occlusal view (x 3).



P_4 — There is a small posterior accessory cusp on the flange of the main cusp. The posterior lander is tridentate (length=1.3, width=2.8).

Comparison— The P^1 from the Love local fauna is slightly larger than the P^1 from the tapotypic late Cretaceous Black Rock Ranch local fauna, Orma Valley formation, California and the P^1 from the Cretaceous South Tejon Hills, Orma formation, California, described by Tedford and Taylor (1963). It has a more prominent metastyle than is either of these two specimens. The preacropus is more prominent than in the California material. The hypostome is not as long posteriorly as in the Tejon Hills specimen (the hypostome is broken in the Black Rock specimen).

The P^1 is smaller and more rectangular than is Protoproctos Hispanocorys from the early Mesozoic East local fauna of Texas (Tedford and Taylor, 1963). The cusp is more acute, the preprotacrita and preacropus better developed and the hypostome more prominent and more anterior-ventrally situated. In development of the metastyle and other characters the P^1 from the Love site bears a strong resemblance to Protoproctos, the latter exceeds it.

The P^2 from the Love site is smaller and lower crowned than the specimen of P. parvum from Black Rock Ranch, but agrees with it in morphology. It is not as square as the P^2 of P. ligandoceras and has better developed external and preacropus and a more internal hypostome. The small size of this tooth from the Love site indicates the possibility that it may belong instead to another faun such as Ligandoceras.

Family Pteromalidae

Leptocryptus clauderianus, n. sp.

Fig. 32, Table 34.

Biology. UF 24724, right dentary fragment with \bar{L}_1 , \bar{P}_{2-3} , \bar{R}_1 .

Specimens. UF nos. 24587, left P^A , 24588, right P^A , 24589, left P^A , 24590, right P_2 , 24591, right R_2 , 24592, left dentary fragment with \bar{L}_1 , 24593, left dentary fragment with \bar{P}_{2-3} , \bar{R}_{1-2} , 24724, holotype, 24594, left dentary fragment with \bar{R}_1 , 24595, dentary fragment, 24596, left and right side fragments; all from the Love Bone Bed, Alachua County, Florida, late Clauserian-Late Hemul Age.

Descriptions. P^A . The protcone is large, subequal in size to the paracone. A well developed hypocone and the protocone are separated to the paracone by a crest. The paracone-entocone blade is unetched. The prestyle is subequal in size to the entocone. There is a small median cusp on the anterior cingulum. There is a moderate posterior cingulum and the lateral cingulum is weak to absent.

P^I . The protocone, paracone, entocone and ectocone are subequal in size. The paracone and entocone are anterior to the protocone and ectocone. There is a small mesostyle on the posterolateral border of the tooth and a very small mesostyle. The hypocone is on the posterolateral border of the tooth, medial to the protocone.

Figure 32. Isotermic condensation. (A and B) of 24403, P^d , enclosed and external view (x 2); (C) of 24403, left dentary fragment with L_1 , external view (x 2); (d) of 24403, P_2 , internal view (x 2); (E) of 24021, right dentary fragment with C_1 , P_2 - R_2 , external view (x 2);.



Table 26. Measurements taken on *Isostichus capillatus*.

SP no.	24105	24517	24955	24704	24602	25055	24601
P^A length	10.5	9.5					
width	10.5	9.5					
P^B length			10.8				
width			10.2				
P_2 length				3.5	3.4		
width				2.7	2.6		
P_3 length				4.0	5.3		
width				4.6	4.4		
P_4 length				3.0	6.0		6.8
width				5.2	5.4		5.2
P_1 length				11.2	11.4		
width				6.2	6.2		
P_2 length					4.2	6.4	
width					4.4	5.6	
P_2+P_3					20.8	(22.7)	
depth below P_1				14.8	16.2	16.1	

The direction for the P_3 is lateral to the alveoli for P_1^1 and P_2^2 . These two alveoli are anteroposterior on the medial border of the ramus at the symphysis. The center is deeply grooved medially at the base of the enamel to antero-medially at the top. There is a small diastema between the caninus and P_3 .

P_3 is a small tooth with two, possibly fused, roots. There is a small posterior accessory cusp. P_3 has a well developed anterior accessory cusp on the posterio-external flank of the main cusp. The anterior cingulum is narrow, the posterior cingulum broad. P_4 is larger than P_3 and has a relatively larger posterior accessory cusp and better developed anterior and posterior cingula.

Even though the P_3 's are only slightly worn, the cusps are all subequal in height and are connected by cristae or nearly equal height. The paracanal and metaconal are close together. The triserial opens laterally through an upside-down S-shaped notch between these two cusps. There is a wider labial opening for the buccal talonid between the metaconal and metaconid. There is a small hypoconulid on the posterolateral cusp connecting the hypoconal and anticonal. The hypoconal is connected to the protoconal by a cristid oblique. There is a small antero-labial cingulum and a restricted posterolabial cingulum.

The P_5 is small, oval in outline, and double-rooted. The paracanal is small, the protoconal and metaconal are connected by a convex posterior cingulum. The talonid is reduced to a posterior heel.

The mandible is heavy and increases slightly in depth anteriorly.

There is a large orbital foramen beneath F_2 , a smaller one may be located somewhat posteriorly. The ventral border of the mandible is constricted beneath the masseteric foramen. The ventral border of the masseteric foramen widens posterolaterally.

Left and right otic fragments, presumably from the same individual, are assigned to L. floridana after comparison with L. maculata. The bulla is ventral in shape, but is skewed anteriorly. It is fixed to the surrounding bones. The auditory tube is very long, passing ventral to the long and broad posterior root of the tympanic. The external auditory meatus has a circular cross-section. The paroccipital and the much larger external processes are broken off, but they both appear to have been joined to the bulla. The large stylomastoid foramen lies between the occipital process and the bulla. An unusual feature of this auditory region is that the canalis musculotubarius opens ventrally into the foramen ovale. The posterior carotid foramen is in the antioxypterus, approximately halfway between the median and posterior lateral foramina. The middle lacerate foramen is posterior to the common opening of the foramen ovale and canalis musculotubarius. The petrosquamosal foramen divides in two internally. One opening communicates medially and dorsally with a foramen in a depression on the posterior root of the tympanic adjacent to the bryostoma wall.

The right otic fragment is broken medially, revealing the internal structure of the bulla. Two septa radiate medially and anteriorly, respectively, from the elongate ventral lip of

the crista typanica ventrally to the floor of the bulla. A smaller third septum extends posteriorly from the radial septum. The canal connecting the former sylvianotubular primitive and defurcation forms a relatively large tube on the inside of the typanic chamber. This tube and the dense septa partition the ventrolateral portion of the typanic chamber. The epitypanic recess is a deep pit. The fossa muscularis major is extremely large.

Comments. The most striking difference between the bullae of L. atalaphae and L. flaviventris is the absence of bony projections. There is an additional septum in the interior of the bulla of L. flaviventris and the epitypanic recess and the fossa muscularis major are large and deeper. In both, the foramen ovale and the ovalis musculotubularis share a common opening.

Intermedia canadensis most closely resembles Intermedia arizonae from the Elwoodian Ash Hollow Formation, near Big Springs, Nebraska (Matthew, 1924). Both possess well developed anterior cingula and have produced posterior accessory osses on P_3 and P_4 . Intermedia canadensis is larger than L. arizonae (P_4 length 6.8, width 3.2) and has better developed posterior accessory bulks on P_{3-4} .

The P^8 of L. flaviventris is more quadrate than in L. arizonae, L. missouriensis, L. atalaphae or L. arizonensis, and has a much better developed parasphenoid ligament. The lower premolars have well developed posterior accessory osses and anterior cingula than L. arizonae or L. atalaphae. As in the P^8 , the P_3 has a much reduced

shearing function with the talpid more closed than L. griseus or L. accipitrinus, and with the cusps of the lateral equal in height to those of the trigonid.

Two other specimens appear to be referable to Lepidarcus. Floridanus. One is a T_2 from the late Clarendonian Black Rock local faunas of California. Macdonald (1946) described this specimen as a *procyonine*, but also discussed the possibility that it might belong to an advanced species of Lepidarcus. The specimen is similar in size and morphology to the Florida material. The other is a lower jaw fragment with $M_{1,2}$ from the late Clarendonian Black Butte local faunas of Oregon (Macdonald, 1946). This specimen was described as Elphidotyles, sp., but has been reidentified as a specimen of Lepidarcus (Ogden, 1970). It most closely resembles the Florida specimens or all the described material.

TRANSITION. The left and right jaw halves (JP 34704 and 24421), although not found together, may belong to the same individual. They are similar in size and degree of wear of the teeth. These two jaw halves are much larger in size than anterior jaw fragment JP 34423 (Fig. 35). The culms of this jaw fragment is considerably smaller than that of the holotype. It is not likely, therefore, that this size difference is a result of age differences. The alveoli of the anterior jaw fragment indicate that the teeth in this specimen were slightly smaller than those of the holotype. This difference could be the result of individual or sexual variation. Macdonald has suggested that "siggatus," (Gerr, 1944) is a uniform male specimen of Lepidarcus griseus, a possibility noted

as uniformly by Borr, with its enlarged symmetrical structure and large canines. The lower jaw sample offers further evidence of sexual dimorphism in aggression.

Exoskeleton, head Fig. 1 Antennae (Methuen and Bailey)

Fig. 110-F, Table 25

Antennae (antennae), 1st seg. 25432, left 2nd, 25433, 25434, right coxites with P₁, 25435, 25436, edentulous mandibles, all from the lower river bed, Alachua County, Florida, late Cretaceous-Late Eocene Age.

Description. The occlusal surface of the 2nd is concave transversally and is expanded apically. The internal border is convex. The canines are very long. The paracane is connected to the slightly smaller ectacane. The ectacane is somewhat inferior to the paracane. The anterior empodium is greatly expanded anterior to the paracane. Four denticles are present at the locations of the remainder of the teeth. The large, transversally oval paracane is situated close to the anterior border. The hypacane occupies the internal border and a round ectacane's hypacane is present midway on the posterior border. There are three roots: a large triangular root and two labial roots. The root beneath the ectacane is smaller than the root beneath the paracane.

The alveolus for the lower canine is relatively large. There is no alveolus for the P₁. P₂ is offset labially. P₃ is slightly shorter than P₂. P₄ is labially compressed. The posterior

Table 25. Measurements taken on *Uthmaniyia cf. U. laeta*.

	BP no. 1	29402	29403	29404
H^1 length	18.4			
width	12.2			
P_4 length			11.6	11.4
width			5.6	5.2
P_2-P_1			(66.7)	(64.9)
P_2-P_3				(61.8)

secondary cusp is located slightly lateral to the midline of the tooth. The anterior cuspules is narrow, the posterior cuspules broader. M_1 is elongate, M_2 is single-rooted. The mandible is elongate. There are two mental foramina; a larger one beneath the P_2 and a small one beneath the P_3 . The mesosternite fossa extends to a point between M_2 .

Comparison. This material and Thamnophilis laticus are taxonomically assigned to Elanoides because of their elongate mandibles, narrow cheek teeth, and especially because of, as indicated by the skull, the narrow elongate M_1 , a generic character. The mandible is not as deep or massive as in the genera Proctos and Paralimna and the premaxilla are more slender. Elanoides laticus was described from the Claibornean little white river fauna of North Carolina as Proctosomus laticus (Matthew and Bailey, 1903) and was later assigned to the genus Brachygnathus by Gregory and Davis (1911). Brachygnathus has a short, deep jaw and a short, broad M_1 . Thamnophilis laticus is known from a jaw with P_2 and P_3 and between P_4 and M_1 . The mandible and teeth of Thamnophilis laticus are approximately equal in size to the material from the late Iowian bed. The only significant difference that is observable is the absence of a P_1 in the Florida material. A P_1 is present in other species of Thamnophilis.

The syntopic species, Thamnophilis robustus (Cope), is a lower jaw from the Salentine formation of Fort Mifflin, Nebraska. The P_1 and M_1 are badly broken. The M_2 possesses a transverse heel. It is much smaller than the Florida material.

Sphenotilia boltoni Rathbun from the late Devonian Green Creek formation of Nebraska is much smaller than the Florida material. The P_4 is a relatively more slender and sharper tooth, with the posterior heel not as broad or well developed. P_5 has a prominent setacoid.

Sphenotilia dolichops Rathbun from the early Devonian Clinton formation of Nebraska is smaller than the Florida material. P_4 has a poorly developed posterior accessory cusp and posterior alingulum. The mandible is deeper than in the Florida specimens. P_5 has a poorly developed setacoid.

Sphenotilia jacksonensis Sherwell from the Clintonian Black Belt facies is much smaller than the Florida material. The posterior accessory cusp of the P_4 is very weakly developed. The setacoid of P_5 is large and the telodid slightly beaklike.

Discussion. The wear facets on the P^1 (Fig. 10F) indicate that a large, well developed setacoid was probably present on P_1 . The P^1 of Ischnotilia (radialis) is unknown, but is presumably similar to that of Ischnotilia, which has a similar P_1 . The P^1 of Ischnotilia has a posteriorly directed external alingulum which is widest between the paracusp and setacoid, a setacoid that is distinctly smaller than the paracusp, no telodidote, and a large central protodote. The protodote articulates between the protoconid and hypostome of P_2 . The lower P^1 has a large oval anterior wear facet. The external part of the facet probably articulates with the protoconid of P_2 , the internal part, with a large setacoid. The broken surface of the P_1 of P. laticus is expanded lingually at the posterior

Figure 22. *Ischyropsis (Ischyropsis)* sp. (A - C) of 25614, $\times 1$, internal, occlusal and external views (A 1.85); (D) of 25625, left dentary fragment, external view (x 1.15).



Differences and comparisons. Brown (1988) described Jackia gregaria as a new genus of radiolarian radiolite from the probably late Cretaceous Eocene(?) Formation of Washington. She distinguished Jackia from Eucylindria on the basis of its shallower jaw, taller, more translucent processes, and absence of spines. Edwards (1988) reported a radiolite of Jackia from the late Cretaceous part of the Santa Rosa Group, California.

Telford et al. (in press) consider Jackia to be a junior synonym of the European subgenus Isoperidites (Oligodites), which was raised to rank as genus in the Cretaceous. Hinde (1987) established the subgenus Oligodites for the North-western I. clausenae and the Atlantic I. baileyi. Isoperidites (Oligodites) baileyi (Fitch, 1981) is known from a P^3 and an R_2 that appears to be indistinguishable from that of Jackia.

The R_2 from the Lave site is larger than that of I. gregaria and smaller than that of I. baileyi. The radiolite is more massive than that of I. gregaria and the R_2 appears to be relatively lower than a slightly more sublaterally directed main cup.

Etymology na.

Referred material. BP 23306, right P^3 , from the Lave Bone Bed, Alaska County, Florida, late Cretaceous Late Paleol Age.

Description. The P^3 is a small, internod-externally elongate tooth (Fig. 21c). There are three roots [large internal and subnod-internal roots and a small postnod-external root]. The

process is joined to and is slightly external to the subequal sized nucleus. The external claspule is almost external to the process. The pedicel is low and is connected to the anterior border by a propodeolate. There is no distinct hypocost on the convex internal border (length 2.1, width 1.1).

Classification. This H^1 was covered with the H^1 's of *Acron* material in the collection of the AMNH. It most closely resembles the H^1 of *Clasiusella* in morphology and size. For that reason it is assigned to this genus.

CONCLUSIONS

Eleven taxa of Carnivora are described from the latest Clarendonian Late Miocene Red Hook local fauna, Alachua County, Florida. The Late Miocene Red Hook consists of fluvialite sediments of the Alachua formation that fill a complex stream channel system cut into the underlying Tertiary of the late (upper) Crystal River Formation (Smith et al., 1980).

The genus Archaeocynopsis and the genera included by Bonstedt (1988) in the subgenus are removed from the Felidae and placed in the Miacridae. The Miacridae are characterized by a primitive masticatory locking system and by a specialized dentition. The Miacridae are not considered to be Felidae.

The new carnivorid species, Archaeocynopsis livesi, is intermediate in size between A. agassizi, best known from the middle Clarendonian of Nebraska, and the early to middle Miocene A. brachy. Archaeocynopsis livesi is referred to the late Clarendonian (Late Miocene) Red Hook local of California and the early Miocene (Early Miocene) local fauna of Nebraska. It is referred to A. (sensu) Archaeocynopsis livesi and is a long-snouted carnivore with a semi-digitigrade posture. Archaeocynopsis probably had prey substantially heavier than its own body weight, including large ungulates such as Helicotyles and Antilocapra.

A new Peltid species, *Xenopeltis pallens*, is known only from the Love Note Bed local Fauna. Like it and *P. hirsutipes*, known from the late Clintonian and early Neoproterozoic, probably share a common ancestor which was derived from a form similar to the middle Devonian *Pycnolophus intermedius*. Current and available of *P. pallens* demonstrate that this species was sexually dimorphic.

The new genus of pteropod, *Archaeopoda*, is known from Burlington through Neoproterozoic age deposits from western North America and Florida. Five new species of *Archaeopoda* are described, including the geosynaptic species *A. floridana* from the Love Note Bed. *Archaeopoda* is most closely related to the North American late Pliocene through Pleistocene pteropods of the *Gemma* group.

The new proposed genus and species, *Pteropoda hirsuta*, is possibly ancestral to the two latest genera *Pteropoda* and *Synopoda*. All three genera have the singular process of the mandible situated above the level of the mandibular tooth row. *Pteropoda* is characterized by the presence of large double-rooted P_1 's.

Helicopoda forms, the geosynaptic species of the berythine valid *Helicopoda* is recognized as a member of the *Helicopoda* *hirsuta* species group. The generic name *Helicopoda* has priority for the taxa that were included in the *Helicopoda* *hirsuta* species group. Two species of *Helicopoda*, *H.* cf. *hirsuta* and the larger *H.* cf. *hirsuta*, are recognized from the Love Note Bed local Fauna. There is much variation in size and spacing of the promarginals and in the degree of accessory cusp development in *H.* cf. *hirsuta*. This genus is similar in size and morphology to *H. hirsuta* from the middle and

late Cretaceous of Nebraska and South Dakota. In Florida early Neopliocene local faunas such as those's and Atlantic form, small species of Spizella are replaced by Elanoides.

Elanoides cf. humboldt is much rarer than E. cf. gracilis in the lower bone bed local fauna. This large species is not as abundant in the assemblage of the P_4 and reduction of the P_{1-3} is significant from the early Neopliocene of Texas, Colorado, Nebraska or Florida referred to Spizella colinus.

The small sized species, Protonotaria cf. nebulosa is known elsewhere from the late Cretaceous thick rock Ranch local fauna. The P_4 from Florida is slightly smaller than the California material.

A new species of mactalia, Lophoceros spinosus, most closely resembles L. spinosus from the Cretaceous Ash Hollow Formation of Nebraska. A P_4 from the late Cretaceous thick rock Ranch local fauna of California and a lower jaw fragment from the late Cretaceous thick bone local fauna of Oregon are probably referable to L. spinosus.

The other three mactalia are poorly represented. Elanoides near E. gracilis is similar to E. gracilis from the Cretaceous Ash Hollow Formation of South Dakota. Elanoides (nebulosa) is known elsewhere in North America from the late Cretaceous and early Neopliocene. Elanoides is known from Nebraskan through Neopliocene deposits.

The Cretaceous from the lower bone bed support the latest Cretaceous age assignment for this fauna (Sible et al., 1960). Elanoides (spinosus) migrated from Eurasia to North America in the late

Chondrodonta and ranges through the early Ancepsithian. Barbaroschilia longi is intermediate in morphology between S. worrilli from the early late Chondrodonta Ash Hollow formation of north-central Nebraska and S. frieki from the early Ancepsithian. Barbaroschilia longi also occurs in the late Chondrodonta Black Rock Ranch local fauna of California and the earliest Ancepsithian Jewett local fauna of Oklahoma.

Specimens of agasszi and S. cf. bayleri are at a comparable stage of evolution as those now known from the late Chondrodonta upper Ash Hollow formation. Sagardius concoloratus, Postagasszi cf. neodonensis and Hypanchitia near H. laeta also support a late Chondrodonta age assignment for the Love Bone Bed local fauna. Early Ancepsithian invertebrates such as ground sponges and brachiopods are conspicuously absent in the Love Bone Bed local fauna.

The Love Bone Bed local fauna provides the first picture of late Pleistocene vertebrate community organization east of the Mississippi River detailed enough to allow comparison with the contemporaneous fauna of the Plains. Three classes of taxonomic distinctions between the Love Bone Bed local fauna and contemporaneous midcontinent faunas can be recognized: 1) taxa unique to Florida; 2) earlier records of taxa than those of closely related forms in the midcontinent; and 3) later records of taxa already extant in the midcontinent. Each of these distinctions reflects differences in geography, ecology or both.

Both endemic and early occurring taxa of the Love Bone provide evidence of a Florida or Gulf Coast endemic fauna which may also be

an extension of the poorly known late Miocene faunas of Central America. Sampling errors alone might explain the absence of early occurring Florida taxa in contemporaneous faunas of the Plains, but this seems unlikely, especially for large vertebrates, in the well sampled western faunas.

All of the plesiomorphic genera at the late site (Jans et al., 1988) are found in the High Plains. Ceratolophosaurus, common in the Plains, is apparently absent at the late site. Of the seven species of horses at the Late site, two are Gulf Coast endemics: Hesperomys montanus is known from the late Miocene of Florida, Mexico and Honduras; Pentapod gladius, from Florida and Mexico. Among the cervids, unique taxa include Peromyscus and Stenomys collaris. Elasmotherium lancei, Elaphus cf. harrisi and E. cf. hyndsi are all represented in the faunas of the plains. Peromyscus cf. montanus, Elasmotherium montanus, and Thomomys cf. T. harrisi appear to be closely related to taxa from western faunas. The other small cervids are the poorly known from anywhere but occurrences to be made even on a generic level.

Certain elements of the fauna appear to have Neotropical affinities. Of the two new primate genera, Peromyscus appears to have evolved in the Gulf Coast province, although a specimen apparently referring to this genus is known from the early Hemipterian of Kansas. Peromyscus, which is related to the South American Peromyscus group, is more widespread both temporally and geographically, but is best known from the Gulf Coastal faunas. One taxon of the Cricetidae (Jans et al., 1988), which are all

probably Florida includes as much as the specific level, is closely related to the Neotropical biogeography and may document the origin of the organisms. The Tlax "Xenodactylus" parvus is another Florida endemic clearly related to South American faun-

The vertebrates of the Love site (Bink et al., 1960) have a high relative abundance of ray fish, especially breakers, that are rare in contemporaneous midwestern faunas. This probably reflects the more arid conditions in the Gulf Coast (Sonoran region [Mexico, 1975]) in contrast to the Plains. This region may have provided a haven for browsing artiodactyls, three-toed horses and arboreal carnivorans. The early and abundant record of the browsing Synsorex at the Love site may have been a result of its evolution in the Gulf Coastal region.

Telford et al. (in press) have stated that the Gulf Coast seems to have been a separate biotic province during most of the Pliocene, based faunal continuity with the Appalachian having been established by Neogene time. During the Clarendonian, Texas evidently became incorporated into the Clarendonian (Great Plains) chronofauna range (Bink, 1974), but it was unclear whether Florida remained a haven for a distinctive mammalian assemblage. The Love faun has local faunal similarities that point. While it does show some evidence of endemism, including special affinity with the Middle American fauna, such distinctions are minor. The major differences from midcontinental faunas are ecological rather than geographic. In the latest Clarendonian Florida had become part of the Clarendonian chronofauna showing a major overall similarity to the faunas of the midcontinent.

APPENDIX

LIST OF PORTLANDS, METALS, OF BRACHIOPODITE LOFT AND CONJECTURE [18]

Brachio-podite [18]. - 18 nos. 25013-25021, atlas, 25021-25022, apical, 25022-25023, scapula, 25024, right lateral, 25025-25027, proximal humerus, 25028-25029, distal humerus, 25030-25031, ulna, 25032-25033, proximal ulna, 25034-25035, radius, 25036-25037, proximal radius, 25038-25039, distal radius, 25040-25041, scapulothorax, 25042, 25043, trapezoid, 25044-25045, scapula, 25046, 25047, scapula, 25048-25049, metacarpal I, 25050-25051, 25052-25053, metacarpal II, 25054-25055, 25056-25057, metacarpal III, 25058-25059, metacarpal IV, 25060-25061, metacarpal V, 25062, pelvis, 25063-25064, pelvis fragment, 25065, femur, 25066-25067, proximal femur, 25068-25069, distal femur, 25070-25071, tibia, 25072-25073, proximal tibia, 25074-25075, distal tibia, 25076-25077, metatarsal, 25078-25079, metatarsal, 25080-25081, metatarsal, 25082, 25083, 25084-25085, metatarsal I, 25086-25087, metatarsal II, 25088-25089, metatarsal III, 25090-25091, metatarsal IV, 25092-25093, metatarsal V.

Brachio-podite [18]. - 18 nos. 25094, atlas, 25095, 25096, scapula, 25097-25098, right lateral, 25099, ulna, 25100-25101, proximal ulna, 25102, 25103, radius, 25104, 25105, proximal radius,

2510-2515, axial relief, 2516-2518, subhorizontal, 2519-2520,
 steep, 2521-2525, unroofed, 2526-2531, reticulate I, 2532-
 2535, reticulate II, 2536-2537, reticulate III, 2538-2540,
 reticulate IV, 2541-2543, reticulate V, 2544-2547, peltic
 fragments, 2548, linear, 2549-2553, pectinate linear, 2554-2555,
 distal linear, 2556-2558, latic, 2559, 2560, pectinate latic,
 2561-2563, axial latic, 2564-2567, subapical, 2568-2570,
 unknown, 2571-2581, vertical, 2582-2587, oolitic, 2588-
 2591, reticulate II, 2592-2595, reticulate III, 2596-2598,
 reticulate IV, 2599-2600, reticulate V

LITERATURE CITED

- Barbour, E. S., and H. J. Cook. 1915. A new water-hooted bat from Nebraska. *Bull. Geol. Surv.* 7:225-226.
- Bonaparte, G. de. 1844a. Essai sur la position taxonomique des genres *Elanoides* Vieill. et *Elanus* Viguer. *Bull. Geol. Surv.* 17:227-228.
- Bonaparte, G. de. 1844b. Remarques sur la classification des *Elanides*. *Bull. Geol. Surv.* 17:229-230.
- Bonaparte, G. de. 1845. Note sur la région méridionale de quelques *Carnivores*. *Arch. Sc. Geneve* 21:253-254.
- Burke, J., and L. S. Burdett. 1975. South American *Carnivora*. In *Fauna of Colombia*, J. Ramirez (ed. F. Mouton). Dr. H. Junk. The Hague 129:1-54.
- Burke, R. 1951. Revision des espèces nord-américaines de *Neotoma*. *Sci. Ann. France Nat. Sci.* 10:265-272.
- Grant, R. 1947. Contribution à la connaissance des genres *Elanides* et *Elanoides* (Carnivores-Elanides). *Trav. Inst. Sci. Univ. Belgrade*. Préhistorique Fac. Sci. Belgrade 8:1-32.
- Gray, L. S. 1931. A new genus of batoid from the Glenrose Formation, Washington. *Los Angeles Co. Mus. Contr. Sci.* 128:1-6.
- Clark, J., and T. C. Townsend. 1932. Ancestral genetic characters as related to the genus *Elanoides*. *Pacific Nat.* 36:3-11.
- Cook, H. J. 1914. A new batoid from the lower Pliocene of Nebraska. *Bull. Geol. Surv.* 7:53-54.
- Cook, H. J., and J. L. Burdett. 1932. New batoides from the Pliocene and Pliocene of western Nebraska. *Journ. Paleont.* 26:540-547.
- Cope, E. D. 1860. On the extinct bats of North America. *Bull. Mus.* 14:253-258.

- Cope, E. D. 1871. On the canines of the Long Fork Spook. *Bull. U.S. Geol. Surv., Territories* 8: 327-330.
- Cope, E. D. 1871. A Lichen-Lick Skiff From the Long Fork. *Bull. U.S. Geol. Surv.* 10: 1619-1620.
- Cope, E. D., and N. D. Merriam. 1871. Tertiary Mammalia and Pterian Vertebrata. *Amer. Mus. Nat. Hist., Monograph* 1: 1-2.
- Cope, E. 1880. On the systematic position of *Phylomyon hesperidius* Peckham and some related forms. *Amer. Zool.* 4: 211-212.
- Delcourt, M. G. 1929. Early Miocene mammals of the Rock Ranch local fauna of Texas. *J. Paleont.* 3: 289-292.
- Dein, B. 1938. Die Fossiliere aus dem Mittel-Pläozän (Mammalia) von Bismarck-Hohe bei Eschbach in Bayern. *Schweid. Bayerische Acad. Wiss., Math.-Nat. Abh.* 32: 1-115.
- Gerr, J. A. 1884. *Phylomyon hesperidius*, a new genus and species of hesperidina mammals from the late Miocene Redwood Valley Formation of Butte, *Ann. Carnegie Mus.* 13: 176-184.
- Gerr, J. A., R. H. Jones, and J. E. Savage. 1954. *Peromyscus hesperidius* in the Cenozoic section of California. *Bull. the Amer. Mus.* 120: 65-71.
- Howard, S. M. 1928. A new side of *Sciurus (Sciurus) hesperidius* from Contra Costa County, California. *Palaeontol.* 20: 1-5.
- Platel, L. 1884. Observations relatives à divers caniniformes fossiles provenant de la Grive Saint-Aignan (Indre). *Arch. Mus. Hist. Nat. Lyon* 2: 3-19.
- Platel, L. 1885. On the value of the characters of the teeth of the canines in the classification of the Order Carnivora, and on the systematic position of *Peromyscus* and other disputed forms. *Proc. Zool. Soc. London*, 1885, pp. 4-26.
- Glénard, L. 1888. *Officiers et origines structurels de (Sciurus hesperidius) paléontol. et Officiers moyen de Science*. G. B. Acad. Sci. Paris 323-324-325.
- Glénard, L. 1891a. Le Fossé des caniniformes éoliques de l'Indre (Indre). *Mus. Mus. Nat. d'Hist. Nat.* 15, sér. C, 2: 1-19.
- Glénard, L. 1891b. Placodontes et diploodontes chez les caniniformes *Thalysidius*. *Mammalia* 25: 1-11.
- Glénard, L. 1944. Les Améliorations des Placodontes de l'Indre. *Ann. Mus. (Paris)* 12: 23-44.

- Kribsburg, I. 1938. *Sarcosaurus yersakovi*, n. gen., n. sp., a fossil cynodont from the Karabagion de Ligne. C.R. Acad. Sci. (Ser. Biol.) France 168:23-24.
- Lanyon, R.J. 1978. Functional implications of aden-boosted foetal morphology. *Neurobiology* 2:302-312.
- Lanyon, R.J. 1979. Functional implications of foetal foetal morphology. *Ann. Anat.* 162:111-121.
- Graham, A. 1975. A review of the origin and historical recognition of floristic affinities between Asia and eastern North America, in Floristic and paleogeographic of Asia and eastern North America (ed. A. Graham). Amsterdam, Elsevier, pp. 1-18.
- Graham, A. 1975. Late Cretaceous evolution of tropical lowland vegetation in Veracruz, Mexico. *Evolution* 29:323-336.
- Gregory, J.C. 1932. *Ptilosoma vertebrale* from Big Spring Canyon, South Dakota. Univ. Calif. Publ. Geol. Sci. Ser. 34:307-344.
- Gregory, J.C., and T. Brown. 1931. *Reptiles and Ptilosoma* from the Late Cretaceous of Texas. *Geological Survey of the United States* 1:1-15.
- Hesse, C.G. 1943. A *Ptilosoma vertebrale* from Big Spring, Texas. *Univ. Tex. Publ.* 1943:475-485.
- Hillman, C.W. 1943. The occurrence of *Ptilosoma vertebrale* in the Big Spring, Texas. *Trans. Am. Mus. Nat. Hist.* 85:245-252.
- Hughes, J.B. 1943. The auxiliary region in some members of the *Procyonidae*, *Canidae*, and *Ursidae*. Its significance in the phylogeny of the Carnivora. *Bull. Amer. Mus. Nat. Hist.* 85:253-271.
- Hughes, J.B. 1953. Auxiliary region in North American fossil *Procyonidae*. Its significance in phylogeny. *U.S. Geol. Surv. Prof. Paper* 268:95-115.
- Hux, E.W. 1978. The auxiliary bulge in *Canis*: An anatomical basis for reappraisal of carnivoran evolution. *Jour. Morph.* 143:21-34.
- Hux, E.W. 1979. Cranial anatomy of *Canis* Jordan (Therapsid: Carnivora), an *Asiaticus* *Asiaticus* from the Miocene Basin, France. *Jour. Paleont.* 53:612-622.
- Jordan, E.S. 1935. A skull of *Asiaticus* *Asiaticus* from the early middle Pliocene of France. *Jour. Paleont.* 9:1028-1030.

- Smith, G.B. 1927. A Pliocene vertebrate fauna from Elgin County, Ontario. *Bull. Geol. Surv. Ont.* 46:1-27.
- Smith, G.B. 1938. *Stenoniscus*, a new genus of Pelyidae from the Pliocene of California, Texas and Ontario. *Ann. Mus. Nat. Hist.* 34:375.
- Stephenson, G.B., and A.B. de Góssyal. 1935. Los proceros argentinos del género *Chelonicolites*. *Bolet. Mus. Argent. Cienc. Nat. Bernardino Houder*, 1935. 1:1-35.
- Stephenson, G.B., and G.B. Berg. 1936. Un nuevo proceros del Plioceno de Las Playas (Provincia de Córdoba). *Rev. Assoc. Geol. Arg.* 1936:221.
- Leidy, J. 1868. Notice of remains of extinct Vertebrata, from the valley of the Middle River, collected during the exploring expedition of 1857, in Nebraska, under the command of Lieut. G.B. Warren, U.S. Top. Eng., to Dr. F.B. Hayden, geologist to the expedition. *Proc. Acad. Nat. Sci. Philadelphia* 18:20-27.
- Leidy, J. 1868. The extinct mammalian faunas of Nebraska and Colorado. *Jour. Acad. Nat. Sci. Philadelphia*, 2nd ser., 7:3-122.
- Macdonald, J.B. 1944a. A new species of *Hyopsalopus* from the Upper Pliocene of Nebraska. *Bull. Calif. Acad. Sci.* 42:45-52.
- Macdonald, J.B. 1944b. The Pliocene carnivores of the Black Hawk Group. *Bull. Calif. Acad. Sci.* 42:63-80.
- Macdonald, J.B. 1945. Review of the Pliocene Mammal Bone Fauna of southeastern South Dakota. *Bull. Los Angeles Co. Mus. Nat. Hist.* 6:1-62.
- Rehn, F.B. 1926. Dental morphology of the *Hyopsalopus* with a description of *Conradiodus* nov. gen. *Field Mus. Nat. Hist. Geol. Ser.* 9:223-230.
- Rehn, F.B. 1944. The *Hyopsalopus* genus group. *Bull. Field Mus. Nat. Hist. Geol. Ser.* 2:75-87.
- Reynolds, L.T. 1944. The Pliocene (Mammal, Davidson's Fort 1, The systematics of *Hyopsalopus* and *Prohyopsalopus*. *Bull. Amer. Mus. Nat. Hist.* 131:115-219.
- Burtin, L.B., and C.B. Schultz. 1975. Scheffer-boothed cats, *Hyopsalopus* and *Hyopsalopus* from the Pliocene of Kansas and Nebraska. *Bull. Univ. Calif. St. Mus.* 18:55-67.

- Ballou, W.D. 1930. The phylaxia of the Felidae. Bull. Amer. Mus. Nat. Hist. 25:255-258.
- Ballou, W.D. 1933. Third contribution to the Santa Cruz Fauna. Bull. Amer. Mus. Nat. Hist. 58:69-210.
- Ballou, W.D., and R.J. Coyle. 1939. A Pliocene fauna from western Nebraska. Bull. Amer. Mus. Nat. Hist. 25:383-414.
- Ballou, W.D., and J.A. Philip. 1934. New or little known mammals from the Museum of South Dakota. American Museum expedition of 1933. Bull. Amer. Mus. Nat. Hist. 28:334-353.
- Ballou, W.D., and R.A. Stebbins. 1935. Osteology and affinities of *Homotherium*. Univ. Calif. Publ. Bull. Dept. Geol. Sci. 15:171-211.
- Baskin, J.C. 1964. Species groups of the world genus *Adelaptes*. (ed.) Soc. Amer. Ornithology Section Progress No. 25. Austin: Austin, p. 43 (color-1).
- Bellett, J.B. 1917. Paleobiology of North American Eocene (Kansasite, Orodonta). Contrib. Vert. Evol. 1:1-134.
- Borison, J.C. 1935. Tertiary mammalian faunas of the Mojave Desert. Univ. Calif. Publ. Bull. Dept. Geol. Sci. 15:327-383.
- Borison, J.C., and E. Stueck. 1938. Reptiles of Rancho La Brea. Carnegie Inst. Wash. Publ. 422 (1-231).
- Broderi, L.B., and R.B. Telford. 1973. The *Cantharctinae*, a new group of extinct aquatic Caninivores and a consideration of the origin of the *Cantharctidae*. Bull. Amer. Mus. Nat. Hist. 151:203-229.
- Patterson, C., and R. Prosser. 1972. The fossil mammal fauna of South Africa, in *Evolution, mammals, and southern continents* (ed. A. Kruuk), pp. 247-385. State Univ. N.Y. Press, Albany.
- Prosser, J. 1931. Carnivora. in *Treatise on Paleontology* (ed. J. Prosser), 4:445-535.
- Prosser, R.J. 1921. The western characters and classification of the *Procyonidae*. Proc. Geol. Soc. London 1921:387-422.
- Stacy, E. 1938. *Homotherium diadematus*, a new dog from the Pliocene San Bern Co. Calif. Santa Fe, California. Univ. Calif. Dept. Geol. Sci. 24:263-268.
- Storer, A.S. 1964. Vertebrate paleontology. Third ed. Univ. of Chicago Press, Chicago and London.

- Schlosser, R. 1917. Die Affen, Lemuren, Monopitheciden, Insectivoren, Marsupialier, Greifvögel und Carnivoren des nördlichen Territoriums und deren Beziehungen zu ihrer Lebenswelt und Fauna der nördlich-amerikanischen Tierwelt. 71. Beitr. zur Ges. Naturk. 1-1-223.
- Schultz, E. P., R. A. Schuller, and L. B. Martha. 1936. A new tribe of sub-fossilized cats (Felidae) from the Pliocene of North America. Univ. Calif. Publ. Zool. 1: 1-25.
- Smith, W. S., and G. L. Jepsen. 1935. The mammalian fauna of the White River Oligocene. Part 1. Marsupials and Carnivores. Trans. Amer. Phil. Soc. n.s. 26: 1-155.
- Smith, W. S., and H. F. Osborn. 1935. Preliminary account of the fossil mammals from the White River and Kaipar Formations, described in the Museum of Comparative Zoology. Bull. Mus. Comp. Zool. 29: 25-122.
- Snyder, M. 1943. The solitary region of the arctoid carnivores. Field Mus. Nat. Hist. Zool. Ser. 28: 30-69.
- Stewart, J. A. 1943. The Quaternary faunas: Studies in earth history and paleoecology. Trans. Amer. Phil. Soc. 33: 1-27.
- Simpson, G. G. 1944. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist. 79: 1-xvi, 1-258.
- Stricker, H. F., S. B. Skinner, and E. J. Gooss. 1937. Stratigraphy and lithology of late Cenozoic deposits in central Idaho County, western Idaho. Bull. Amer. Mus. Nat. Hist. 75: 223-256.
- Stewart, E., and V. L. Vanderhorst. 1903. *Onychomys*, a new genus of dogs, and its relations to *Sceloporus* Cope. Ber. Calif. Acad. Sci. Zool. Ser. 23: 179-188.
- Stock, C. 1938. Canid and proboscidean remains from the Pliocene deposits, Redwood Grove, California. Carnegie Mus. Nat. Hist. 193: 41-47.
- Storrs, J. P. 1936. Adaptations of rineopsis to arid carnivores (Mammalia). Syst. Zool. 25: 263-274.
- Storrs, J. P., and J. Huxley. 1934. Review of some carnivores (Mammalia) from the Thomas Farm (local fauna) (Hesperomys, Hesperomys, Hesperomys). Amer. Mus. Nat. Hist. 1934: 1-8.

- Telford, S. G., T. Schuch, R. F. Steamer, S. J. Taylor, S. K. Fields, J. A. McMichael, T. A. Patton, J. A. Riedinger, and S. J. Meltzer. 1959. Faunal succession and ichthyofauna of the Miocene through Pliocene (Tertiary interval) [late Oligocene through late Pliocene epochs], North America. Univ. Calif. Publ. Geol. Sci. in press.
- Telford, S. G., and S. Taylor. 1959. A cladistic analysis of the Cadeite. Bull. Amer. Mus. Nat. Hist. in press.
- Tellard de Claville, P. 1918. Les Poissons de Grèce—Les Poissons Péloponn. Publ. Inst. National. 18 3-38.
- Tanner, H. H., Jr. 1945. Observations relating to some of the faunas of the state of the coast to America, and on the classification of the order Caracidae. Proc. Zool. Soc. London, 1945, pp. 42-55.
- Randall, J. E. 1931. *Scorpaenidae* (Pisces) from the marine territory of California. Univ. Calif. Publ. Geol. Sci. 21:15-24.
- Randall, J. E., and J. J. Gregory. 1936. A review of the genus *Scorpaenidae*. Univ. Calif. Publ. Geol. Sci. 29:143-154.
- Pillajo, J. P. de, and H. Oyarce de la Cruz. 1945. Contribución al conocimiento del *Aluconellus* (Pisces). Com. Sup. Cient. Cienc. Conf. Cient. Pilla. pp. 7-44.
- Rivet, J. 1934. Catalogue ichologique de la Faune des mammifères, oiseaux de la Grèce (Sous-Afrique), Sous Arch. Mus. Hist. Nat. Lyon 3:1-193.
- Wagner, H. 1918. A new species of *Pseudogobius* (Pisces: Caracidae) from California. Journ. Paleont. 9:127-129.
- Wilde, S. G. 1934a. The Eury and Heterocentrus (Eurycentridae) fossilian faunas of north-central America. Univ. Calif. Publ. Geol. Sci. 29:1-117.
- Wilde, S. G. 1934b. The Pliocene Caracidae of Florida. Bull. Fla. St. Mus. 14:312-326.
- Wilde, S. G. 1937. A history of known vertebrates in the New World Part I. North America. Am. Mus. Nat. Hist. 5: 355-565.
- Wilde, S. G., R. J. Paffenhof, and J. A. Jackson. 1955. Spines and osteology of the Late Eocene fish from the late Pliocene of Florida. Amer. J. Sci. in press.

- Wills, J. A., 1940. Miocene carnivorans, Texas Gulf Coastal Plain. Journ. Paleont., 35, 1803-1820.
- Wortman, J. A., and M. B. PARRISH, 1951. The ancestry of carnivoran members of the Canidae, the Viverridae, and Procyonidae. Bull. Amer. Mus. Nat. Hist. 52, 129-138.

BIOGRAPHICAL SKETCH

Jon Alan Rudin was born February 18, 1941, in Boston, Massachusetts. He received a B.S. degree from New York University in 1960 and an M.S. degree from the University of Arizona in 1965. Since September, 1965, he has been pursuing the degree of Doctor of Philosophy in zoology at the University of Florida. While in residence at the University of Florida he has held teaching assistantships from the Department of Zoology and research assistantships from the Florida State Museum. His present research interests include the systematics of late Tertiary rodents and carnivores.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



David Wells, Chairman
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



Edward S. Gentry
Graduate Research Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



David Wells
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



Edward S. Gentry
Associate Professor of Zoology

This dissertation was submitted to the graduate faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

March 1985

Dean, Graduate School